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THE EVOLUTION OF MECHANICAL IDEAS[1]

THE EVOLUTION OF MECHANICAL IDEAS IN ANCIENT GREEK THOUGHT

PROFESSOR HARRY BEAL TORREY
STANFORD UNIVERSITY

IN the more than twenty-five centuries through which the current of mechanical ideas may be said to flow, at least three waves of interest have lifted themselves above the general level and moved forward at a quickened pace. The first of these culminated in the fifth century before Christ; the second, after a prolonged period of comparative calm, more than 2,000 years later; while the third, especially characteristic of the last two hundred years, has not yet reached its crest. Upon these three waves in turn, the discussion of the morning will be centered.

First of all, let me tell you, as a sort of explanatory preface to my remarks, how I conceive the term *mechanism* as applied to both physical and biological science.

A scientific mechanism is never properly thought of as inviting an ultimate explanation. It is a device of the investigator and subject to description. But it can be described approximately only. What the investigator tries to do is to reduce his description to its simplest and most general and widely applicable form, in terms of verifiable factors. His success is measured by his rate of progress toward that goal. It does not help him to insist on factors that he can not verify or perceptually approach. His indispensable tool is the working hypothesis. What he can approach with such a tool and reduce to physicochemical terms he is likely to regard as mechanical. But

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the word is not itself essential. My purpose in this symposium is to trace as helpfully as I may the history of certain epoch-making attempts to improve our control of perceptual data by reducing them to the most general and inclusive descriptions involving the fewest possible assumptions and the largest future significance.

The first philosophical conceptions of a mechanical universe that have been preserved in the scattered and fragmentary records that have come down to us appear abruptly, about 600 B.C. in the speculations of a small group of thinkers who made their home in Ionian Miletos. It is unlikely that their revolutionary views were entirely without anticipatory sources. Their true history, however, is dim with conjectures, through which it may help us to find the most probable path by recalling the origin of Miletos itself.

Its founders have been traced to one of several separate southward migrations of Greek-speaking peoples who began to leave their homelands to the north of Greece centuries before the Trojan War. They marched roughly over the more sophisticated cultures of their predecessors on the Grecian peninsula, bringing with them their Olympian gods, who thrived there for centuries. Their language took permanent root. Some of them settled down, to be absorbed ultimately into the population they had dispossessed. Others pushed on, from island to island, across the Aegean, establishing themselves in time in a chain of city states and island communities along its eastern shore, from the Dardanelles to Rhodes and Crete and Cyprus. Aeolian invaders gained a foothold to the north. Those who spoke Doric Greek favored the southern coast and adjacent islands. Between them lay a region still unoccupied by Greeks. And here the Ionians established themselves. Here they wiped out a Caro-Lelegian Miletos and built their own close by, near the mouth of the River Meander, whose valley, extending toward the east, gave the higher lands of the interior easy access to the sea. Strategically placed, with a good harbor and an enterprising population, this new Miletos became in due time a bustling, prosperous cosmopolitan center for wide-rang-

ing commercial activities and philosophical exploration as well. Phoenicians, Carians, Lydians, Mesopotamians, Syrians and Jews mingled familiarly with the dominant Greeks and spoke their language. Milesian ships planted colonies on the shores of the Black Sea and in the delta of the Nile. Paper was first obtained from Egypt, with whom visits of travelers were exchanged. Both commodities and ideas came from distant places to the east. Coinage, adopted from Lydia, made it easier for trade and the accumulation of wealth in private hands, which brought power and a certain freedom from despotic political control. Great temples were built according to Olympian traditions; but there was no priestly class to enforce conformity either in religious doctrine or practice. To this significant fact should be added the well-known capacity of the Greek mind for abstract and impersonal thought that comes out in especially strong relief when the contributions of the Milesian physicists and their successors are compared with the self-centered cosmology of contemporary Hebrew scriptures. While the opening chapters of Genesis were providing an unimpeachable social rating for mankind, Thales and his friends were seeking a stable basis for thought and action in new and impersonal conceptions of the cosmic process.

We may attempt to refer these differences to differences of environment, especially customs and pursuits; and with reason. With reason, also, we may take account of differences of blood. Both, in my opinion, play significant parts. It is easy to imagine the birth of science, however speculative, in an alert, cosmopolitan community pressed with practical problems involving large interests and depending for their solution on straight thinking and long-time predictions. But it is easy to believe that into so timely an environment, timely men must come. In the days of Homer, the human forbears of Miletos recognized no pressing necessity for a scientific world. The problems of life, as the Iliad pictures them, were simple and circumscribed, the actors (even wily Ulysses) naive. Law to them was such as might be imposed by parent or by tribal chieftain, personal, whimsical, arbitrary, inconsis-

tent, expected to achieve results without revealing processes. Such, also, were the acts of the gods, unpredictable but influential. The part of human wisdom lay in skilful supplication, not in understanding. When Achilles before the body of the slain Patroclus feared lest flies should enter his gaping wounds and breed worms therein (Iliad, xix, 23), he was reassured by the promise of Thetis that though Patroclus' body should lie exposed for a year, the flesh would be sounder than ever. Comforted, he ranged the host; for Thetis was not only his mother, but a goddess as well.

How the bard privately regarded the gods of whom he sang is not altogether clear. I am willing to believe that his tongue was occasionally in his cheek on their account. There can be no doubt that they lingered as literary devices long after they had ceased to be taken seriously in any other role; for it is so with our own mythologies. Long before the days of the Ionian physicists, common-sense minds may well have grown increasingly dissatisfied with the record of the gods in practical affairs; this mood persisting until superior substitutes had been suggested by imaginations bold and keen and practical enough to point the way to more successfully pragmatic modes of thought.

II

It is here that Thales enters, though far less suddenly and dramatically than appears to us in the perspective of time. About his life and interests he left not one written word. According to the fragments that ancient commentators have rescued from a fast-fading tradition, he was a Greek, possibly with some Carian blood through a father whose people had long been assimilated by the dominant race. In Miletos he was known as an active man of affairs who watched the weather and its effect on the market; as an engineer who was once employed by Croesus; as a statesman who proposed a federation of Ionian cities for the common defense, and won a place among the Seven Wise Men; as a traveler who brought back from Egypt the crude rudiments of practical geom-

etry used in measuring the land; as an observer of the stars who taught mariners to steer their courses by them; as a student of Chaldean astronomical records by means of which, by rare good fortune, he successfully predicted an eclipse.

So, when we contemplate him in his more abstract moments, conceiving the world in its ultimate nature as a self-contained mechanism composed of but one substance —water—from which all else had been and could be derived without external agency, there is evidence for the probability that such speculations were his answer, in the most general form, to the perplexing questions that an exceptionally varied and active experience had forced upon his practical mind. It is quite unlikely that the scraps of his views that Aristotle was able to salvage for us adequately represent the whole. The significance of his contribution to the history of science can hardly be said to lie in the particular world-stuff that he selected. What he sought was a tangible basis for understanding, that should reduce the multiformity of a changing world to order and make prediction possible. This he found in a universe that was, first of all, self-sufficient, forever freed from supernatural caprice; that was also fundamentally simple and unitary, despite its phenomenal variety; and that, so far as we know, was indifferent to distinctions between mind and body, life and not-life. Finally, he proposed water as the substance that should successfully embody these conceptions; and in doing so, raised the only issue that distinguished him from his otherwise loyal Ionian successors.

Anaximandros of Miletos, younger than Thales and possibly his pupil, proposed as a substitute for water—which itself needed explanation—a vaguely defined substance which he called the Boundless (*to apeiron*). It was infinite in extent and inexhaustible in amount, eternal, indestructible, always in motion. From it everything else had been ultimately derived, and to it would ultimately return. And this applied to innumerable worlds distinct from our own. Beyond these fertile conceptions of in-

finity and change, Anaximandros' special views of the development of the cosmos are of minor importance to our present problem. He was the first to associate the heavenly bodies with rings or wheels that were remnants of spheres developing out of eddies in the *apeiron*. These rings and spheres were physical entities, like the spheres of Aristotle, not the mathematical relations by which Aristotle's friend Eudoxus accounted for the motions of the sun, moon and stars. Anaximandros' conception of an earth suspended freely in space was more abstract, although it was a discoid earth not out of conformity with the geographical knowledge of the time.

His successor Anaximenes turned to air as the primary substance, a change less reactionary than it sounds. For with it he introduced the idea of condensation and rarefication, which made it possible to derive all discrete bodies as well as all sorts of substances from different degrees of condensations of a single one. In one of the sayings imputed to him by Aetius he struck the following physiological note: "Just as our soul, being air, holds the body together, so do breath and air encompass the whole" (EGP75).

During the next century there was a wide-spread interest among philosophers in the bodily mechanisms. But these were preceded by more general reflections on the creation of the living world, which it will be desirable to examine first. In doing so, it should be kept in mind that to the Ionians, the primary cosmic substance was at once animate and inanimate. It had not yet occurred to them to make the distinction, and transformations of one into the other, in either direction, presented no theoretical difficulties at all.

When therefore Anaximandros announced the origin of living organisms from water, it was only in keeping with the tradition in which he had been reared. When, however, he made the further announcement that in the beginning, man himself had been a fish, he became a pioneer, in the minds of many commentators, of organic evolution. The story is, if Plutarch is to be believed, that Anaximandros, having observed the pseudo-placental attachment of

the young of certain viviparous sharks to the wall of the maternal oviduct, noted its resemblance to the placentation of the human foetus *in utero*. By assuming that man, in the beginning, was the offspring of a shark, Anaximandros was able to reconcile the creation of air-breathing man with a water origin. Man's life as a fish was limited to a period of gestation only long enough to bring him to a maturity consistent with an independent terrestrial life. Once he stepped on land the episode ended.

All of which indicates that we are dealing here with a creation story involving a type of organic metamorphoses commonly recognized in Anaximandros' day. Man emerged from the shark as butterflies emerge from the pupal cases of caterpillars, as other insects emerge from plant galls, and shall we say, Eve from Adam's rib. Anaximandros, though unquestionably a *potential* racial evolutionist, appears never to have suspected the meaning of such a phrase as Darwin's *descent with modification*.

This conclusion must be drawn also from the more elaborate speculations of Empedocles of Sicilian Acragas on the origin of animals. His, too, is a creation story, to which the term evolution has more than once been confusingly applied. According to Fragment 17, there were two periods of creation and of passing away. In the first, the parts of animals arose separately, and came together by chance. Without fulfilling any cosmic design, therefore, monstrous forms arose, some of which were too under-privileged to live; others of which persisted, within the limits of this period, as chimeras of various sorts, apparently to account for old beliefs in their existence. However fantastic the story, the mechanical sieve-like process characteristic of natural selection is clearly manifest in it, but without any relation whatever either to racial evolution or the problem of species.

In the second period of creation, "whole-natured forms first arose from the earth, having a portion both of water and fire"; without limbs "nor yet the voice and parts that are proper to men" (Fr. 62). Higher organisms succeeded them in due time; but without hint of derivation either from them, or from each other. This conception of

a series of independent creations from a common substrate is not "descent with modification." Though Empedocles was not an evolutionist, he deserves especial attention for his introduction into the creation of the living world a mechanical conception that was to recur twenty-two hundred years later as a much more potent answer to the doctrine of design.

When we turn from this impersonal conception of nature to Empedocles himself, we find him, by his own confession (Fr. 112), an egotist, something of a swaggerer, fond of the adulation of the mob, tempted to oracular discourse, and not above suspicion, according to his critics, of downright charlatanry.

In the Hippocratic corpus one finds no such hint of personal character. The authenticated treatises breathe a spirit of straightforwardness and candor for physicians in every age to emulate. Clinical histories are spread without reserve before the reader, whatever the results of treatment. The treatises on wounds and fractures are full of keen observations that at times led the author close to the realities of infection. But these he never quite grasped and entirely neglected in Epidemics I and III. Oddly enough, it was a contemporary historian who first made the observations that had eluded the physician. In Book II, Chapter vii, of "The Peloponnesian War," Thucydides has written as an eye witness a masterly description of the famous plague of Athens that is one of the great classics in the annals of epidemiology. Of the physicians in that epidemic he says, "they died themselves the most thickly, as they visited the sick most often." Farther on he says: "Yet it was with those who had recovered from the disease that the sick and the dying found most compassion. They knew what it was from experience, and had now no fear for themselves; for the same man was never attacked twice—never at least fatally" (Crawley tr.). These passages alone make it clear that Thucydides had not only recognized infection, but immunity as well.

But the Hippocratic writers made other notable contri-

butions to the evolution of mechanical ideas in biological science, two of which I will mention here. The first established the status of all diseases as natural phenomena, and specifically repudiated magical and divine causation. In the second, the author unmistakably anticipates both Lamarck and Darwin. After describing ("Airs, Waters, Places," xiv) the custom among the race called *Longheads* of binding the soft heads of infants in such a way as to increase their length, he quaintly remarks that in course of time "custom became nature," and bandaging was no longer needed to achieve the desired result. This is a clear anticipation of Lamarck. Then the author goes on to account for the facts in terms of a mechanism that is a counterpart, in a sentence, of Darwin's "provisional hypothesis of pangenesis": "For the seed comes from all parts of the body, healthy seed from healthy parts, diseased seed from diseased parts. If, therefore, bald parents have for the most part bald children, grey-eyed parents grey-eyed children, squinting parents squinting children, and so on with other physical peculiarities, what prevents a long-headed child?" Again, in discussing epilepsy ("The Sacred Disease," v), he says: "Its origin, like that of other diseases, lies in heredity. For if a phlegmatic parent has a phlegmatic child, a bilious parent a bilious child, a consumptive parent a consumptive child, and a splenetic parent a splenetic child, there is nothing to prevent some of the children suffering from this disease when one or the other of the parents suffered from it; for the seed," etc.

These few examples will suffice to illustrate some of the forms under which mechanical ideas appeared in the biology of the period. Others will be indicated incidentally in the following paragraphs.

III

The gods whom the Ionians sought to exclude from any causative relation with the cosmic process linger among their successors in the form of more or less abstract substitutes. Empedocles recognized two external corporeal

existences (Love and Strife) that entered into the inert world as activating principles. The primary fusion of substances from which Anaxagoras derived his universe was stirred into action by a much more tenuous substance with special powers—his *Nous*. A century later Aristotle conceived a metaphysical device known ever since as the Prime Mover to communicate eternal motion, again from without, to his finite spherical universe in some entirely non-mechanical way.

In complete contrast was the plastic, entirely self-contained and exclusively physical conception to which Leucippus and Democritus were led in attempting to provide the monistic universe of the Ionians with an all-sufficient mechanism of differentiation. It will be convenient to discuss the views of both of these innovators together, remembering, however, that Leucippus was the pioneer, Democritis the keen and sensitive elaborator of their bold and uncompromising speculations.

They accepted from their Milesian predecessors a single primary substance, such as the *apeiron,* that was homogeneous and eternal. But by a brilliant stroke of genius they imagined it in atomic form, composed of solid particles, indivisible and unalterable, infinite in number, differing only in shapes and sizes, and moving spontaneously and freely in empty space—the so-called Void. If perchance their purposeless movements brought them together and entangled them with each other, mixtures would be formed with properties dependent on the numbers, shapes, sizes, motions and arrangement of the atoms involved. This was the mechanical basis for the creation of all the composite bodies of the universe, however great or small. They were in a sense only temporary aggregates. They could appear, grow and transform, diminish, disappear. In the living world, as in the non-living, life and death, development and decay were at bottom only expressions of atomic integration and disintegration. The atoms alone were immortal.

No fundamental distinctions, indeed, were made between living and dead, and body and soul, and sensation

and thought. All were interpretable in atomistic terms. The atoms of the soul were spherical, like those of fire; present probably to some degree in all objects but essential in the living. Since all mixed bodies gave off atomic effluences, soul atoms were lost in this way, especially by the living, and replaced by a sort of porous respiration. Sensations not obviously referable to contact were roused by effluences from the stimulating body. Thoughts arose similarly; they were never spontaneous. Both sensory data and the thoughts engendered by them were, however, to be regarded with reserve as true representations of reality. Subjective experiences like color, for instance, were mere convention; only the object from which the impression emanated was real and true.

Criticize these conceptions as we can and may, it is difficult to withhold warm admiration from this valiant but premature attempt to apply to the whole content of human experience a purely mechanical explanation in so daringly simple a form. Plato, however, turned to Democritus a shoulder that was both cold and indifferent. Aristotle treated his views with more consideration, yet with the opposition to be expected from one who conceived the universe as an unbroken continuum in which all events were interpreted in terms of immutable forms and final causes; in which there was no theoretical opportunity for cosmic evolution or, among organisms, of specific change.

In spite of the adverse weight of Aristotle's prestige, however, the essentials of atomism found their way, through Epicurus and Lucretius, to the threshold of the Christian era. Then for more than fifteen centuries they retired to the comparative obscurity from which they were rescued by Gassendi, who brought them to the notice of contemporary scholars. Galileo gave them a sympathetic reception. Robert Boyle used corpuscles closely resembling the atoms of Democritus in his thinking; and so did Newton. So also did John Dalton, who, at the opening of the nineteenth century, discovered the law of multiple proportions with their aid. In his hands they appear to have reached the status of a working hypothesis.

THE EVOLUTION OF MECHANICAL IDEAS IN THE PHYSICS AND CHEMISTRY OF THE NINETEENTH CENTURY[1]

DR. FREDERICK OTTO KOENIG
STANFORD UNIVERSITY

A SURVEY of the rather complex evolution of mechanical ideas in the physics and chemistry of the nineteenth century is suitably introduced by some remarks on the role of mechanics in physical science in general.

The science of mechanics is that which deals with mass, force and motion. It was founded in the seventeenth century chiefly by Galilei, Huygens and Newton. At the hands of Newton it received in all essentials a form it has retained ever since. The form of mechanics is that of a deductive theory based on certain laws or principles, which are treated as axioms. As such, mechanics constitutes the most perfectly developed branch of any science not purely mathematical. This fact is not altered by the circumstance that the axioms of mechanics are at present undergoing extensive revision through the theory of relativity and the quantum theory.

Now if the ideas of mechanics had led to nothing beyond a deductive scheme, which, however perfect, included only a limited range of phenomena, these ideas would not interest the biologist at all, and the chemist and physicist much less than they actually do. What, then, is the source of the great interest that physicists, chemists and biologists have for the ideas of mechanics? It is, of course, a second aspect of mechanics: mechanical ideas serve to *correlate* different classes of phenomena, not obviously mechanical in themselves, more effectively than ideas drawn from any other branch of science. In short, mechanical ideas are the natural tools for the logical unification of science, of which we hear so much these days.

At any given time, the mode of this unification, that is, the relation of mechanics to the particular classes of

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physical and chemical phenomena, varies greatly from one such class to another.

In the simplest, most favorable case, the phenomena in question can be deduced by applying the laws of mechanics to an assumed mechanical model. In this case we say, the phenomena have been *explained* by mechanics. Thus the physicists of the middle of the nineteenth century explained the laws of gases—a class of phenomena—through the kinetic theory, which assumes gases to consist of swarms of elastic particles, separated by distances on the average great compared with the particle sizes, exerting no appreciable forces on each other except during collision, and obeying the laws of mechanics.

In other cases, however, the relationship of physical or chemical phenomena to mechanics is not so simple as to merit the term explanation. Thus the phenomena of electromagnetism have never been satisfactorily explained on a mechanical basis, as have the laws of gases. Several attempts to arrive at such an explanation, starting from assumed mechanical properties of the ether, were made, to be sure, between 1865 and 1900, but in the present century relativity theory and quantum theory have shown these attempts to be futile. Actually the complete elucidation of the relationship between electromagnetics and mechancis is one of the hard nuts theoreticians are still trying to crack. The point of importance from us here is, that although mechanics does not explain electromagnetics, there does exist a relation, for without the mechanical concepts of force or energy, electromagnetism can not be discussed at all; furthermore, whatever logical connection there is at present between electromagnetics and the rest of physical science arises from this relation.

It is for reasons of this kind that I speak in general not of the *explanation,* but merely of the *correlation,* of physical and chemical phenomena, by the ideas of mechanics.

The history of science since 1600 shows that the empirical discovery of physical and chemical phenomena and laws and their theoretical correlation have proceeded simultaneously. The two processes have been mutually

dependent, for theoretical correlation not only implies empirical discovery; it has also exerted a guiding influence upon the course of such discovery. Since its inception about 1600, however, the correlation of empirical results through mechanics has not gone on at a uniform rate. Rather has it been accomplished in a small number of gigantic strides. Of these strides of mechanical theory, the two greatest are generally recognized to be the Newtonian synthesis of 1687 and the discovery of the law of conservation of energy between 1842 and 1847. It is the latter more than any other single development of the nineteenth century which makes that century important in the progress of mechanical ideas in physics and chemistry. I therefore begin the survey of this progress with the law of the conservation of energy.

The conservation principle is due chiefly to three men, Mayer, Joule and Helmholtz, who arrived at it in different ways.

The approach of Mayer, who first stated the principle in 1842, was that of intuition. Mayer realized intuitively that a rational causality sufficiently general to include the phenomena of mechanics, heat, electricity, magnetism and chemical affinity known to his time, necessitates the conservation not only of mass, but also of something else, which he called force. He accordingly declared that "forces are indestructible, convertible, imponderable entities." This principle, although derived from speculation, was applied by Mayer in a strictly scientific manner to a variety of problems, in particular to the calculation of the mechanical equivalent of heat from the heat capacities of gases. In later publications Mayer extended his ideas, but his achievement remained practically unnoticed until attention was called to it by Tyndall in 1862. The fact hit upon by Mayer, that the conservation law is a requirement of scientific thought, has been emphasized subsequently by critics such as Mach, and is at present being illustrated by the argument about the existence of the neutrino, which is merely a hypothesis necessary for the applications of the conservation law to radioactive processes.

The approach of Joule to the conservation law was from the side of experiment. In 1840 Joule had discovered the law relating the strength of an electric current to the heat generated by it. In 1893, unaware of the work of Mayer, Joule published experiments indicating an equivalence between work and heat. In a postscript to his paper of 1843 Joule concludes "that the grand agents of nature are by the creator's fiat indestructible." Joule was led to carry out his experiments on equivalence by the hypothesis that heat is nothing but the motion of the assumed small particles of matter. Joule refined and extended his experiments, and in 1850 published his results on the mechanical equivalent in a great memoir which brought about general acceptance of his views.

Helmholtz wrote on the conservation principle in 1847. He knew of the work of Joule, but not that of Mayer, and so his contribution is less original. Helmholtz's approach is that of the theoretical physicist. Starting from Newton's laws of mechanics, Helmholtz proves that for a system of particles subject to central forces, the loss in potential energy equals the gain in kinetic energy. This result, together with the assumption that heat is molecular motion governed by central forces, leads Helmholtz to a concise mechanical explanation of the equivalence discovered by Joule. Helmholtz then goes on to apply the principle of conservation to electrostatics, electrochemistry, thermoelectricity and electromagnetism. In each case he deduces laws capable of being tested by experiment. Helmholtz is thus the first to demonstrate the value of the conservation principle as a tool for theoretical investigation, and to show in detail how various branches of physics and chemistry are correlated through the principle. Helmholtz's work contains a number of errors to which he himself later called attention.

We forget nowadays that the unification of physics and chemistry brought about by the conservation principle was something very revolutionary. Actually it implied the destruction of the entire existing system of physics and its replacement by another system, whose basis, form and chances of success seemed uncertain to many thinkers of

the time. The system dethroned by the conservation principle was that of the so-called imponderables. These imponderables are readily recognized as extensions of the Empedoclean-Aristotelian concept of element, a preeminently non-mechanical concept. Heat was supposed to be a weightless fluid, of which nothing was known, except that it had the properties of heat. Similar conceptions were held concerning electricity and magnetism. In accord with this theory, physics in the eighteenth century had consisted of an array of absolutely disconnected subjects —mechanics, heat, electricity, magnetism, optics. The conservation principle destroyed the segregation, replacing the physics of matter and a set of unrelated imponderables by the physics of matter and energy, both conserved, both capable of existing in a variety of forms. Energy, moreover, was a concept derived from mechanics.

The conservation principle came suddenly and unexpectedly to most of the scientists of the time. To us, however, it appears as the necessary result of an extensive series of empirical advances. By 1842, the steam engine had long suggested the existence of relations between heat and mechanical work. The discovery of Coulomb's law in 1785 had related electricity and magnetism respectively to mechanics. Electricity and chemical affinity had been inter-related through the phenomena of galvanism discovered by Galvani and Volta between 1786 and 1800, through the preparation of the alkali metals by Davy in 1807 and through the quantitative laws of electrolysis discovered by Faraday in 1834. In 1820, Oersted had discovered the effect of electric currents on magnetic poles, in 1822 Seebeck the thermoelectric effect, in 1831 Faraday electromagnetic induction, in 1840 Joule the law for the heat generated by the electric current. Thus the internal boundaries of eighteenth century physics had really begun to yield to empirical attack before the arrival of the conservation principle. The principle was therefore not only the seed of future progress, but also the fruit of previous discoveries. It was the mechanical rationalization of the empirical necessities of its time.

Mechanical ideas were extended in the nineteenth century not only through the conservation law, but also, to a lesser extent, through numerous other developments of physics and chemistry.

Outstanding among these developments of secondary importance is the atomic theory, which furnishes a mechanical model for chemical processes. Until advent of the atomic theory, chemical processes had seemed almost as mysterious as those of life. From a philosophical speculation the atomic theory was transmuted into a working hypothesis of science when Dalton in 1808 used it to explain the empirical quantitative laws of chemical combination and to give a table of atomic weights. Dalton's theory was inadequate to the ideas of its time in one respect—it neglected the distinction between the atom and the molecule of a chemical element. The remedy for this defect was supplied in 1811 by Avogadro in his hypothesis that equal volumes of gases under similar conditions contain equal numbers of molecules. The ideas of Avogadro, however, were disregarded until the resulting confusion in 1860 forced upon chemists their adoption, at the suggestion of Canizzaro.

The chief applications of the atomic theory in the nineteenth century occurred in organic chemistry. This development began with the discovery of isomerism by Leibig and Wöhler in 1823, progressed through the discovery of organic radicals by the same authors in 1832, the discovery of substitution of Dumas in 1839, the development of the so-called type theories by Dumas, Laurent and Gerhardt in the 1840's, and culminated in the theories of valence and molecular structure enunciated by Frankland, Couper and Kekule between 1852 and 1865. In 1874, the theory of structure was brilliantly extended by Van 't Hoff and Le Bel, who, on the basis of the discoveries of Pasteur and Wislicenus regarding tartaric acid and lactic acid, respectively, correlated optical isomerism with molecular assymetry.

In spite of these remarkable successes, the mechanical model furnished by the atomic theory was regarded scep-

tically by nineteenth century chemists, as a mere working hypothesis which might at any time have to be discarded. The present complete entrenchment of the atomic view is a twentieth century achievement. It might be added that except for the dualistic or electrochemical hypothesis propounded by Berzelius and destroyed, in its original form, by the discovery of substitution, the nineteenth century left the problem of the nature of the chemical forces between the atoms practically untouched. All progress in this field has been made in the present century.

Loosely related historically to the chemical atomic theory is the kinetic theory of gases. This theory began when Joule, in 1851, calculated the average velocity of hydrogen molecules at 0° C. It was further developed by Krönig's derivation of the gas laws in 1856, Clausius' attempt in 1857 to relate rotation and vibration of the gas molecules to the heat capacity, and Maxwell's discovery of the law of distribution of velocities in 1860. The relation of the kinetic theory to mechanics I have already pointed out.

The next development that must be mentioned is the second law of thermodynamics. This generalization grew out of the reflections of Carnot, published in 1824, concerning the theoretical efficiency of heat engines. Assuming the impossibility of perpetual motion, Carnot proved that all reversible engines working between the same temperatures have the same efficiency and that therefore "the motive power of heat is independent of the agents employed to develop it." These conclusions, combined with the conservation principle, at that time unknown, would have amounted to a statement of the second law. Carnot did not live to establish the connection. This was first done by Clausius in 1850. In 1848, meanwhile, Thomson had shown that the ideas of Carnot lead to an absolute scale of temperature, and in 1851, Thomson, too, independently of Clausius, arrived at the following correct statement of the second law: "It is impossible by means of inanimate material agency to derive mechanical effect from any portion of matter by cooling it below the tem-

perature of the coldest of the surrounding objects." As a tool for solving theoretical problems the second law was perfected through the introduction of the concept of entropy by Clausius in 1865. From 1869 onwards the second law was applied to the study of chemical phenomena by Horstman, Gibbs, Helmholtz, Van't Hoff and others. The genesis of the second law from the steam engine surely revealed from the start a relation with mechanics. But the nature of this relation appeared to grow ever more mysterious until in 1877 Boltzmann suddenly clarified it. By an extension of the methods of the kinetic theory, Boltzmann *explained mechanically* the second law of thermodynamics, showing it to be merely the statistical consequence of the mechanical behavior of the large numbers of small particles supposed to constitute matter.

Next must be mentioned the wave theory of light. This theory, originated by Huygens in the seventeenth century, was revived in 1802 by Young in order to explain mechanically the phenomenon of interference discovered by him. In 1821 Fresnel, in order to explain as well the phenomena of polarization, introduced the hypothesis of transverse ether waves and developed the theory to a high degree of mathematical perfection. In this form the theory was brilliantly confirmed by the discovery of conical refraction by Hamilton and Lloyd in 1833 and by the measurements of the speed of light through water by Foucault in 1850. Subsequent discoveries, however, made it evident that the wave theory can not be regarded as an absolute or complete mechanical explanation of optical phenomena. These discoveries were: firstly, the recognition of the electromagnetic nature of radiation by Maxwell and Hertz, secondly the Michelson-Morley experiment of 1887, thirdly, the elucidation of the particulate nature of radiation in the present century. The ultimate relationship between optics, electromagnetics and mechanics has not yet been discovered.

Finally, I mention as significant for the extension of mechanical ideas the electromagnetic theory. This theory was developed by Maxwell in 1865 from the hy-

pothesis, suggested in a qualitative manner by Faraday in 1846, that electromagnetic phenomena are due to mechanical processes occurring in the ether, and that optical phenomena are just a special case of electromagnetic phenomena. Maxwell intended his equations, which received their most striking confirmation at the hands of Hertz in 1887, to be both a concise mathematical description of electromagnetic phenomena and the basis for the mechanical explanation of these phenomena. That as a mechanical explanation they have failed, and for the same reasons as the wave theory of light, I have already pointed out; as a concise mathematical description, Maxwell's equations remain unassailed.

We have passed in review those developments in physics and chemistry which during the nineteenth century conditioned in one way or another major extensions of mechanical ideas. There were in addition a few developments which during the nineteenth century were not brought into relation with mechanics. Since these developments have subsequently been brought into intimate relation with mechanics, and since this fact seems to me to hold out some hope to biology, I shall mention the two most important of these developments. They are spectroscopy and the periodic law.

Spectroscopy, from Fraunhofer's mapping of the solar spectrum in 1815, through its applications to chemical analysis by Bunsen and Kirchoff in 1860 and to astronomy by Huggins from 1863 onwards, down to Balmer's discovery of the first spectral series and Rowland's extraordinary technical refinements in the 1880's, remained essentially an empirical science. It became at one stroke an integral part of mechanics with Bohr's work of 1913.

Similarly, the periodic law, discovered by Mendeleef and L. Meyer in 1869, remained a purely chemical generalization until well into the present century, when it, too, was related to mechanics, in large part, moreover, through spectroscopy.

Although a survey as brief as this must be incomplete,

I can not close without some mention of the applications of exact physical and chemical methods to biological problems.

First, attention must be called to the gradual disintegration, due to the growth of organic chemistry, of the theory that a vital force is necessary for the production of the complex carbon compounds obtainable from living organisms. The first blow struck against this theory, Wöhler's synthesis of urea in 1828, by no means destroyed it. Actually the theory was slowly abandoned as more and more natural products were synthesized. One of the last strongholds of the retreating theory was the fact that organisms were found to be continually converting optically inactive substances, such as carbon dioxide, into optically active ones. That this phenomenon is a purely chemical one was not rendered completely certain until Marckwald and others at the beginning of the century demonstrated the influence which optically active carbon atoms already present have upon the production of new optically active carbon atoms.

The elucidation of the chemical processes going on in living organisms, and therefore the extension of mechanical ideas, was greatly furthered by the work of Bernard. Bernard is the founder of biochemical method. He also discovered important facts. The greatest of his discoveries was made in 1848: the glycogenic function of the liver, which demonstrated that, contrary to the general opinion of the time, not only plants, but also animals, are capable of chemical synthesis.

Next must be mentioned the discovery, chiefly by Pasteur, between 1854 and 1885, of the fundamental facts of fermentation, infection and immunity. Although Pasteur was a vitalist, he did an immense service to mechanism. His bacteriological method is an extraordinary extension of the classical technique of chemistry, that of the separation and combination of substances, to living organisms. His discoveries, on the other hand, constitute the foundation of the concept of biochemical

specificity, the concept, that is, of organisms as systems of chemical reagents which interact in a specific manner with ordinary chemicals and therefore with one another. The fruitfulness of this concept need not be emphasized here.

Very significant, finally, for the extension of mechanical ideas, was the study of the physics of the sense organs, which began in the 1830's with the work of Müller on what he called the specific nerve energies. Müller was a romantic and a vitalist, and he used his discovery, that the general nature of the sensation depends on the sense organ but is independent of the physical nature of the stimulus, to emphasize the subjective aspect of physical phenomena. In spite of this fact, the law of specific nerve energies had for the following generation of physiologists a profound mechanical significance. It suggested that if physical and chemical phenomena are merely sensations, then the physiology of sensation is a problem physical and chemical, and therefore partly or wholly mechanical. It is in this spirit that Helmholtz, a pupil of Müller's, in the middle of the century studied the physics of sight and hearing.

Physical investigations with a similar mechanistic bias were carried out by other disciples of Müller, thus by DuBois Reymond on the electric properties of living tissues and by Ludwig on circulation and secretion.

In conclusion we may say: The nineteenth century presents us with a number of extensions of mechanics through developments in physics and chemistry. The greatest of these extensions of mechanics is that due to the law of conservation of energy, which reformed the entire existing system of physics. Some of the extensions involve the direct incursion of physics and chemistry into biology. The situation is on the whole complex because the manner in which mechanics is related to the different branches of physics and chemistry varies greatly from one such branch to another. This is in part owing to the fact that the correlation between mechanics and those other branches is even at present undergoing evolution.

MECHANICAL IDEAS IN THE LAST HUNDRED YEARS OF BIOLOGY[1]

PROFESSOR WILLIAM E. RITTER
UNIVERSITY OF CALIFORNIA

ANY combination of words, one of which is "biology," implies that living things are involved. All the more is this so if another of the words is "idea." For then the implication is that some of the living things are men. Though certain of the anthropoids probably have experiences quite like ours that we name idea, this is so obscure that for this occasion it seems best to assume that the production and use of ideas implies human animals and no others.

Willy-nilly, then, this symposium commits us to something very similar to the old shopworn controversy of mechanism and vitalism. Twenty-six years ago this very month I took a whirl at this controversy under the query of whether it ever could be settled.

The most I now recall of that discourse was to the effect that the controversy seemed to me one over an illegitimate or pseudo-problem, *i.e.,* a problem that never could be solved in the sense of proving that either mechanism of vitalism is absolutely right while the other is absolutely wrong. It seemed probable therefore that the controversy would just stop after a while from having no reason to continue.

Glancing back over what has since happened in science generally and in my own experience particularly, I am sure I could not then see at all clearly how such an outcome would be possible.

But dare I suggest that the form in which the problem comes to us to-day is confirmatory of my feeling (and I am sure that of some others) twenty-five years ago?

Now to the topic in hand. The application of the idea or the word mechanism to living things dates with special sharpness from Descartes—as is well known.

[1] Symposium before the Western Society of Naturalists, University of California, December 29, 1937.

We may make short shift of this cardinal historical point by referring to some of Descartes' figures. Take his picture of a lad with one foot close to a flame. From the foot a nerve (its tubular character, according to Descartes, not neglected) runs up through leg, trunk, neck, etc., to its proper ending place in the middle of the head (supposedly in the pineal body).

In this as in all the pictures by which Descartes' illustrates the anatomical-physiological portion of his theory he is thinking of mechanism. But a cardinal point here is that he was actually representing organism as well as mechanism whether that term was in his thought or not.

Recall now what this mathematician's physician contemporary, Wm. Harvey, was doing in an anatomical-physiological way. Harvey was showing that whether you call a human or any other vertebrate animal a machine or an organism, what you really have is a natural body composed of many parts combined in such fashion that by their interconnection and interaction they give to the whole a complex of qualities to which the word life or aliveness is applied.

Harvey's work on the circulation of the blood as a ground-breaker in the idea of anatomical-physiological systems that are also vital seems never to have received its due of consideration.

Jump now across an entire century to the work of the full-fledged experimental physiologist, Claude Bernard. As a reminder of what he did that is specially relevant for this discussion I quote a paragraph from Singer's "Story of Living Things": "One of Bernard's greatest discoveries . . . was that the liver builds up from the nutriment brought to it by the blood, certain complex substances which it stores against future need. These substances, and notably that known as *glycogen*, it subsequently modifies for distribution to the body according to its requirements."

This work by Bernard as a ground-breaker in the idea of physico-chemical systems that are also vital seems,

fortunately, on the way to getting due consideration at this time.

If, now, one finds it useful to think and speak of such systems as those discovered by Harvey (morphological-physiological) and by Bernard (physical-chemical) as mechanical, well and good. I can not see the slightest objection to doing so. If, however, in thinking and speaking thus one fails to note that the systems are as peculiarly organic and as truly vital as they are mechanical, he fails to include facts that are at least as essential to the complete reality as are those that he does include.

Jump again now across about another century. Coming thus to our own day and another experimental physiologist, W. B. Cannon.

Cannon's work I assume is so familiar to a group like this as to need little more than the title of his book, "The Wisdom of the Body."

Reflecting on the extent to which work in this realm is concerned with the interconnection and interaction among the visceral organs—intestinal tract, blood vessels and blood, liver, spleen, kidneys, endocrine glands and autonomic nerves—it would be justifiable, I think, to substitute for the phrase "wisdom of the body" the phrase "mechanical systems that are vital."

A significant fact about Cannon's book is the great extent to which the word "body" refers to the parts, *i.e.*, the mechanisms, contained in the abdomen and thorax, and the slight extent to which it refers to the parts contained in the head and limbs.

By no means would I have this imply that Canon is oblivious or disregardful of the slighted parts. From his major research interests and activities he is justified in thus limiting the idea of body.

But when the man himself, W. B. Canon, and not merely the investigator, is taken into the account—well some book like Herrick's "The Thinking Machine" is necessary as a mate for "The Wisdom of the Body."

Even these few references can not fail, it seems to me,

to remind biologists who have any acquaintance with the history of their realm during the last two and a half centuries, of the great rôle the idea of "correlation of parts" (using a phrase especially current in French studies of last century) has played in that history.

From this point on my presentation will appear brazenly dogmatic. Anything of mitigation there may be to this appearance will be in the brevity of the time for presentation, and the fact that my own work is so largely involved, much of which is available either in print or in manuscript, though definite references are impracticable now.

The word mechanism has a small place in my discoursings. I have preferred organisms. The preference has been due, I now perceive, to my feeling that organism carries with it more than does mechanism, the idea of life, of living. Whether this feeling is entirely justified does not matter for the present. That it was partly justified, however, is much clearer to me to-day than it ever has been before.

The feeling had its inception in a research on the sexless reproduction of a species of ascidians, published in 1896. The particular point was the surprising discovery that the origin of the main neural body (the "brain") was strikingly different from what, according to all previous knowledge, it should be. The creature's need for a brain and its developmental possibilities for producing it were such as to enable it to modify the mode of production quite radically in order that it might continue to hold its place in the classificatory system to which it belongs.

Such was the only reasonable interpretation of the observed facts that I could find.

Preparatory to a statement of how this experience contributed to my idea of mechanism, or organism, as a living thing due to the cooperation of its parts I must tell a little of my restudy of Darwin and his work.

Never till this study had I clearly recognized the significance of the undoubted fact that Darwin had become prac-

tically convinced of the origin of species by transformation before natural selection or any other cause of the transformatory process had occurred to him. That he *was an evolutionist before he was a natural selectionist* had not before impressed me especially.

This fact in Darwin's work resulted, I find it to be demonstrable, from his remaining true to his qualities as a typical, unspoiled naturalist. Such a naturalist is one who follows the business of observing, describing, naming, and classifying the objects of nature, and does this from a perfectly naive acceptance of the sense data he collects and reflects upon.

It is unmistakable from Darwin's work and his own account of it that the epochal concept of the natural origin of living kinds, or species came first and foremost from his observations on animals and plants, living and extinct, as they exist and through almost countless ages have existed, scattered over the earth, its valleys and mountains, its seas and rivers and islands. In his own language the idea resulted from his studies of "natural history" (largely restricted by him to living nature) and of geography and geology.

Attentive study of his works bring out with great clarity that in natural history as he viewed it is included man also in *every* aspect of his nature—in his mental, intellectual, moral and religious; his industrial, governmental and social nature no less than in his nutritial, reproductive and all physical aspects of his nature. At no single point does this appear more sharply, so far as I have noticed, than in his statements about approaching the moral problem from the side of natural history.

(This basic matter I touched in yesterday's program from a quite different angle in my note entitled "A point in the relation between Charles Darwin and Thomas Huxley.")

Notice now what is unescapably implied in this: By applying himself for five years (during the *Beagle* voyage) with almost unparalleled devotion and labor by the

field naturalist's method, to collecting and reflecting on the facts of sensory observation, Darwin arrived at one of the most far-reaching, most humanly influential generalizations that has ever been reached by a member of the human species.

Glance at it from the standpoint of what Descartes had done two hundred years before. Darwin gave full credence but with vastly enlarged factual knowledge to Descartes' conception of human mechanism (body) arrived at largely by mathematical reasoning. But instead of conceiving, as Descartes had done, thought and everything else of highest worth to man, as belonging to a realm entirely outside of and above that to which mechanism (body) belongs, Darwin gave full credence also to "thought and everything else of highest worth to man," but, on the basis of his vast observational and reflective studies of both mechanism (body) and thought, conceived both to belong to the same realm and to be inseparably dependent each on the other. The supposed other realm outside of and above that of human mechanism on which Descartes staked so much, was too ill described, too dubiously named, and too imperfectly classified, to satisfy the sense preceptional knowledge and the thinking of the Darwinian brand of "colossal intelligence."

I revert now to the idea of correlation of parts in living beings, and refer to another of my own studies in this realm. My book, "The California Woodpecker and I," soon to be issued from the University Press, embodies a rather full account of this study.

The essence of the idea of correlation presented at length in this study can be epitomized quite briefly. The whole mechanical (bodily) structure and function of these birds and of me is such as to force the conclusion that both of us are what we are, individually and racially, in virtue of the fact that all our respective parts are so closely interdependent structurally and functionally as to make the conclusion inevitable, that neither the birds' parts nor mine could have come into existence independently of the continuous correlation of our respective parts.

The avian class (as represented by these woodpeckers) and the mammalian class (as represented by myself) are peculiarly fitted to illustrate the generalization thus stated. This is especially true as to the head-limbs correlation, these being so extremely different in the two groups as to have stampt them in the course of evolution with special distinctness. And in no particular does this distinctness stand forth quite so sharply as in the brain and fore limbs.

The differentiations and specializations of the avian fore limbs for locomotion in the earth's atmosphere; and of the mammalian, especially the human, fore limbs for tactual exploration and for grasping, holding, and generally manipulating the earth's objects is so amazing as to seem quite unbelievable except for the vast observational evidence everywhere round about us.

Now the structural and functional differences in the brains of the avian and mammalian classes, especially when it comes to particular instances, as my woodpeckers and myself, is so great and corresponds so unmistakably with the difference with the limbs and their actions that I seem compelled to recognize it as an instance of structural and functional correlation of parts in the strictest anatomical-physiological sense.

That investigators, even neurologists of the highest rank, appear to have recognized this correspondence only dimly, seems to me explicable only on the supposition that these students have failed to grasp the idea of correlation of parts in its full mechanico-vital meaning. This failure I suspect is due to failure to notice that the principle of correlation of parts holds in racial evolution as well as in individual function and life.

A sort of paleophysiology as well as of paleoanatomy is implied by the idea of evolution as Darwin held it. There is profounder truth in the idea of "The Living Past" than even J. C. Merriam recognized in his delightful book having that title.

And what seems chiefly essential to a grasp of the principle thus extended is a firmer grip on the ideas of the old

and new portions of the vertebrate brains, and, concomitantly, the idea of the old and the new portions of the minds for which ideas we are more indebted to the neurologists than to any other class of students.

Once again I return to Darwin.

The man left one specially weak spot, that of the nature of knowledge in his natural history view of the human species. While he clearly regarded man's mind with all this implies, as part-and-parcel of man's nature, and hence as a proper subject for the natural historian to study, he never tackled the problem of epistemology in a detailed way. He seems to have regarded it as metaphysics and as such quite unsuited to his special interest and ability as a student.

In my own work I have taken his unmistakable implication that the problem really falls within the scope of natural history, and have made a hard and, I think, somewhat courageous effort to supplement Darwin's work in this particular. While it is quite out of the question to give, even in summary, all that my 70,000 word effort contains, I will say this much: With the hope of meeting the criticism, of professional philosophers and theologians of poaching on the almost sacred realm of *epistemology,* I have viewed my study as one of describing in strictly natural history fashion, the getting, the structure, and the using, of natural knowledge.

The one outcome of this study that seems to me of most general importance alike to scientists, philosophers, religionists and anybody else, is that knowing, thinking and understanding are kinds of activity as inseparable from living things as are nutritializing, metabolizing, and reproducing.

Whether the beings performing the vastly varied activities be named mechanisms, organisms or just bodies matters not at all in deepest truth so long as the idea of aliveness or living is recognized as essential to giving them any meaning.

An unescapable deduction from all this is that an effort

to restrict the idea of biology to mechanism with mechanism restricted to the idea of living matter is really an effort to separate the idea of biology from living nature altogether.

Living matter conceived as the adequate cause of plants and animals is not only an empty abstraction; if pushed hard enough it becomes a metaphysical or supernaturalistic idea.

In conclusion I refer to my just published journal article "The Mutually interpretative relation between human and avian natural history." This is an effort to epitomize the results to date of all my efforts in this vast realm, made rather specially on the bases of my study of the woodpeckers and my precious self.

As for myself I find that I am I to my least important sesamoid bones and connection tissue fibers. I am not I because I think (a la Descartes) but because I am a living mechanism (or body as I prefer). Concerning my glycogenic function, in connection with which Claude Bernard made such a hit in research, I do not speak quite accurately if I say "my liver" is the chief operative in the business. The truer statement is that *I* do the trick by means of my liver.

I think now that I can not do better for the very last words of this highly interesting symposium than to repeat the end-most words of the article just mentioned: "Exceedingly greater personal responsibility for my own acts compared with the responsibility of any bird for its acts may be compendiated as the sum and substance of this essay."

MECHANICAL IDEAS IN THE SCIENTIFIC THOUGHT OF THE SEVENTEENTH CENTURY[1]

PROFESSOR EDWARD W. STRONG
BERKELEY, CALIF.

In presenting the nature and rôle of mechanical ideas in the scientific thought of the seventeenth century, I have thought it advisable to limit my discussion to the work of four men. In so doing, I hope to bring out the main features in the development of the master idea of seventeenth century mathematical-physical science. This master idea is the conception of nature as a mechanism. Galileo, Descartes, Boyle and Newton are the four natural philosophers to be discussed. I will be concerned with their model of scientific explanation and with their arguments for the mechanical view of nature rather than with the discoveries and inventions which they made. That is, I will be concerned with the mechanical theory which sprang from and accompanied their scientific work.

There are few contrasts more dramatic in the history of science than that presented by a comparison of Galileo's hypotheses with the world-view of thirteenth century thought. The fundamental conception of the thirteenth century thinker was the idea of nature as a work of art. God had created a world of creatures through the instrumentality of patterns or forms impressed in passive and inert matter. Individual things are the union of form and matter. Since matter is a mere potentiality to receive and distribute forms, the explanation of motion is referred to agents and movers resident in nature. The first Mover and first Cause of all motion is God by whose creative act the world was made. Motions in nature are due to second causes. These causes of vital and intellectual processes—processes with which the medieval thinker was primarily concerned—are entelechies, faculties, and souls. The motion which they produce is ultimately teleo-

[1] Symposium before the Western Society of Naturalists, University of California, December 29, 1937.

logical. In a world designed by a Creator for man, the highest of his creatures, the purposes and ends for which things exist are of central importance. No explanation of nature is adequate without an account of final causes in answer to the question of why things are constituted as they are and why they act as they do. The task of science consists in abstracting forms and arranging them in a system of classification. Classification requires the scientist to distinguish between the inherent, substantial properties of a specie and those qualities which are incidental to it. These doctrines of substantial forms, of inherent properties, of final causes, and of occult agencies were elaborated into a complete theory of nature by Albert the Great and Thomas Aquinas. Therein, Aristotelian science was wedded to Christian tenets of creation and of the two worlds, the one of physical things and the other of spiritual and supernatural essences.

Despite the entrance into Western Europe of Greek and Arabized-Persian science in the twelfth century, and the persistence thereafter of a tradition of mathematical and mechanical studies, little, if any, effect was exerted upon the dominant teleological idea of the Christian philosophers. When we turn to Galileo we encounter a sea-change of thought, a radically different treatment and conception of science and nature. The "Two New Sciences," Galileo's great book on mechanics, is a masterpiece of experimental inquiry and mathematical proof. In it we find the results of observation and experiment theoretically generalized in formulae for the resistance and cohesion of solids, and in laws of uniform and naturally accelerated motion. Historians of science, until recently, have usually regarded the renaissance of Greek science and learning in the fifteenth and sixteenth centuries to be the chief, if not the only, source of Galileo's achievements. There is no doubt that the translation and study of the works of Euclid, Archimedes, Hero, and Appolonius of Perga contributed directly to the advance of mathematics and mechanics. Yet also important were the tech-

nological developments and the material tradition from which Galileo drew. Ernst Mach has summed up admirably the importance of the technological and material conditions of the mechanical science and the mechanistic ideas of the seventeenth century. He recognizes, with Duhem, the rôle of what he calls the "literary heritage" and then continues with this comment:

> But we must consider not only our scientific heritage but also our *material* civilization—in our special case the machines and tools which have been handed down to us as well as the tradition of their use. We can easily set up observations on this material heritage, or repeat and extend those which led the investigators of ancient times to their science, and thus for the first time learn really to understand this science. It appears to me that this material heritage—continually wakening up anew, as it does, our independent activity—is too little esteemed in comparison with the literary heritage. For can we suppose that the paltry remarks of the author of the *Mechanical Problems* about the lever, and even the far more exact remarks of the Alexandrian mathematicians, would not have continually obtruded themselves upon the observing men who were busied with machines, even if these remarks were not preserved in writing?[2]

Galileo himself conveys a similar suggestion in the beginning of the "Two New Sciences" through Salviati, his spokesman in the dialogue.

> The constant activity which you Venetians display in your famous arsenal suggests to the studious mind a large field for investigation, especially that part of the work which involves mechanics; for in this department all types of instruments and machines are constantly being constructed by many artisans, among whom there must be some who, partly by inherited experience and partly by their own observations, have become highly expert and clever in explanation.

Common opinion even by expert artisans, Galileo tells us, is not the proof of observed effects from fundamental principles. The discovery of these principles is the task of the scientist. Two things are essential for this task, one by way of method and one by way of assumption. If there is to be an exact science of mechanics, geometry is required in the use of mathematical instruments by which weight, length, size and other quantities are determined. Measurement alone can translate the physical magnitudes observed into exact amounts. The further rôle of mathe-

[2] "The Science of Mechanics"; Eng. ed. 3; Chicago and London, the Open Court Publishing Co., 1915. Supplement, pp. 13–14.

matics lies in correlating the ratios and proportions of these amounts in figures and equations descriptive of bodies and their motions. Our science is thus a mathematical science. The scientist reasons from the work of machines and the mechanical powers inferred in their operations to the structures of natural bodies and to the forces correlated with the effects he observes. This is not plausible unless it can be assumed that matter is possessed of constant properties which render it subject to rigid and exact mathematical treatment. Galileo explicitly states this postulate. "Since I assume matter to be unchangeable and always the same," he writes, "it is clear that we are no less able to treat this constant and invariable property in a rigid manner than if it belonged to simple and pure mathematics."[3] Mechanics is a mixed science; it is both mathematical and physical. The simple but powerful idea which Galileo followed consisted in the conception that the analysis of a machine is in principle applicable to nature at large; or more simply, that nature is a mechanism analogous to a machine. This conception is significant as much for what it excludes from the science as for what it includes.

A mechanical explanation is limited to the motions and compositions of figured and extended bodies. It excludes, in the first place, an account of effects that are merely qualitative. Put positively, this is the requirement that observed properties be reduced to, or translated into, measured amounts, for only as thus reduced are they accessible to further mathematical demonstration. A mechanical explanation, in the second place, excludes a teleological account of natural processes. This is the rejection of final causes and of agents or movers extrinsic to the mathematical-physical system of nature. Put positively, this is the requirement of Galileo's doctrine of the constancy and invariability of matter. The powers of machines and the forces of nature are materially con-

[3] "Dialogues Concerning the Two New Sciences by Galileo Galilei"; translated by Henry Crew and Alfonso de Salvio. New York, The Macmillan Co., 1914. p. 3.

tained actions. The tension of a coiled spring, for example, is a purely mechanical efficacy in respect to the work it performs. The extension of explanation from machines to nature assumes not only the uniformity of matter but also a similarity of causal factors. The motions produced in natural structures have causes in impact, pressure, cohesion, attraction and other forces comparable to the powers of machines.

I have so far pointed out the place of the mathematical method, of the materialistic assumption, and of the reasoning from machines to natural structures in Galileo's mechanical theory of nature. The account is not complete, however, without a final feature, that of the hypothesis of atoms and vacua.

> Experiment leaves no doubt [writes Galileo] that the reason why two plates cannot be separated, except with violent effort, is that they are held together by the resistance of the vacuum; . . . This being so, I do not see why this same cause may not explain the coherence of smaller parts and indeed of the very smallest particles of these materials.[4]

These ultimate, indivisible, and infinitely small material particles are the constituents of bodies and are subject to the same mechanical laws which hold for bodies. The only difference between atoms and the composites which are formed from them consists in their indivisibility. Their qualities of size, shape, motion and number are precisely those which are examined by the mathematical-physical scientist in his investigation of molar bodies. Galileo's atomism excludes from the ultimate constituents of things all properties but those which are material and mechanical. These are the primary qualities or physical properties brought within the range of the mathematical method essential to an exact science of mechanics. The exclusion of non-material and non-mechanical qualities from scientific consideration is not, for Galileo, an exclusion of them from nature. He does go so far, in his *Il Saggiatore,* as to argue that the non-quantitative aspects of nature are only affects produced in the human mind. Yet it is not in this doctrinal argument but in his method that

[4] *Op. cit.*, p. 18.

the logic of the exclusion of qualities is to be found. The requirements laid down for scientific explanation in mechanics are derived from the nature of its subject-matter and from the procedures of the scientist. Galileo does not maintain that nature is nothing but a vast machine. His mechanical ideas stem from his empirical investigations and extend to the hypotheses and principles necessary for an exact mathematical science of physical effects. The organic world of plant and animal life does not enter into his investigations. The doctrine of the world machine accompanied by an argument for complete and rigid mathematical order and mechanical necessary in nature was first proposed in the modern age by Descartes. His theory is an absolute mechanism as distinguished from the empirical and methodological mechanism of Galileo.

Mathematics, for Galileo, is both operative and abstract. In its operative form, mathematics is the practical geometry of mensuration involving the use of measuring instruments. In its abstract form, mathematics is calculation and demonstration. Galileo held that the principles of a science are never established by mathematics alone. The test of a scientific proposition lies in observation and experiment. Under the actual conditions of empirical investigation, however, the scientist would be confronted with an endless task if he tried to determine all the particular variations of size, shape, motion, and media presented in such a problem as that of the path and rate of projectiles. It follows from this difference between the actual conditions and the mathematical-physical formulae that such formulae or laws are ideal since corrections have to be made in specific cases. The formulae of mechanics are approximately but not absolutely certain in their application.

A neglect of this empirical aspect of Galileo's science and a rationalistic confidence in the mathematical order of nature are characteristic of Descartes. Mathematics takes on a third form which is metaphysical rather than methodological. To attain certainty in the demonstra-

tions of physical science identical to that which held for pure mathematics was Descartes's aim. Such certainty is attainable if we can assume that nature is nothing but extended "corporeal substance" in motion, and that particular figures and movements can be exactly and exhaustively expressed in geometrical relations. Descartes's faith in the latter possibility appears in his statement in "The Principles of Philosophy": "I do not accept or desire any other principle in Physics than in Geometry or abstract Mathematics, because all the phenomena of nature may be explained by their means, and a sure demonstration can be given of them." The common principle of both Physics and Geometry is extension. Figures and motions are treated as modes of this one, basic attribute of matter.[5] The reduction of nature to physical properties that are solely geometrical would make mathematics the master key to unlock all the secrets of the physical world.

This geometrical model, however, provides no scientific explanation of the dynamics of mechanical action. The "object of the geometricians" is, by Descartes, "conceived to be a continuous body, or a space indefinitely extended in length, breadth, height or depth, which was divisible into various parts, and which might have various figures and sizes, and might be moved or transposed in all sorts of ways. . . ."[6] When Descartes came to explain the movement, transposition, or transference, he tried to dismiss the "vulgar sense" of local motion which "is nothing more than the *action by which any body passes from one place to another*."[7] Motion "properly speaking"—and "properly" is here geometrically speaking—"is the *transference of one part of matter or one body*

[5] "Principles of Philosophy," Part II, Prin. XXIII. "There is therefore but one matter in the whole universe, and we know this by the simple fact of its being extended. All properties which we clearly perceive in it may be reduced to the one, *viz.* that it can be divided, or moved according to its parts, and consequently is capable of all these affections which we perceive can arise from the motion of its parts."

[6] "Discourse on Method," Part IV.

[7] "Principles," Part II, Prin. XXIV.

from the vicinity of those bodies that are in immediate contact with it, and which we regard as in repose, into the vicinity of others."[8] The geometry of motion is a relation of places, not a calculation of forces. The dynamics of motion could not be deduced from the geometrical definition of extension. The motion of parts pertains to extension, but the conservation of force is attributed to God, who is thus the Engine of the world machine.[9] God as the Mover is also the Supreme Geometer. The rational order of nature is metaphysically guaranteed in advance. The possessor of correct mathematical equations in a system of universal geometry has a demonstrative certainty in mechanics.

The trilogy of matter, motion, and mathematics with a First Cause in a God of the machine constitutes the absolute mechanism of Descartes. It follows consistently that organic bodies are automata, and that man, except for his rational soul, is also a machine. Descartes likens the organization and functions of the human body to machinery of a fountain activated by a flow of water.[10] Digestion; the

8 "Principles," Part II, Prin. XXV.

9 *Cf.* "Principles," Part II, Prin. XXXVI. "That God is the First Cause of movement and that He always preserves an equal amount of movement in the universe."

The constant amount of motion in matter is correlated with force by Descartes in answer to Henry More's objection to treating motion as simply a mode of matter. If motion is simply a change of place, how can motion pass from one body to another? In his reply, Descartes writes, "When I have said that the amount of motion in matter remains constant, I have understood that of the force impelling its parts, which force now applies itself to some parts of body, and now to others." (Letter X, Quoted in Kemp Smith, N; *Studies in the Cartesian Philosophy,* p. 79). Descartes thus admits the "vulgar sense" which he had tried to exclude in his search for *a priori* mathematical certainty in physical science.

10 "And, indeed, the nerves of the machine that I am describing to you may very well be compared to the pipes of the machinery of these fountains, its muscles and its tendons to various other engines and devices which serve to move them, its animal spirits to the water which sets them in motion, of which the heart is the spring, and the cavities of the brain the outlets. Moreover, respiration and other such functions as are natural and usual to it, and which depend on the course of the spirits, are like the movements of a clock or a mill, which the regular flow of the water can keep up. . . . And finally, when the *reasonable soul* shall be in this machine, it will have its

beating of the heart; nourishment and growth; respiration, waking, and sleeping; sense impressions; the impression of ideas; interior movements of appetites and passions; external movements of the bodily members; all these functions, Descartes states, "follow naturally in this machine simply from the arrangement of its parts, no more nor less than do the movements of a clock, or other *automata*, from that of its weights and its wheels; . . ."[11] The principle of movements in brutes is entirely mechanical and corporeal and "depends solely on the force of the animal spirits and the configuration of the bodily parts." In addition to this principle, there is in man a second principle of movement, the incorporeal mind or soul.

The mechanical laws of matter in motion do not apply to the spiritual substance of mind. Since nature is nothing but a mathematical-physical order, mind is therefore supernatural, or at least extra-natural. Spiritual substance is said to interact with the body though how this is possible, on either the laws of mechanics or the acts of immaterial mind, Descartes was never able to show. The problem of interaction was in fact insoluble by the very nature of the definitions given to matter and mind. The pineal gland through which body and soul are supposed to carry on their interactive transactions is itself physiological and is therefore as divorced from mind as any other part of matter. Not being material, mind is not extended; yet in the mind are all the secondary qualities, those affects produced in it by the figures and motions of physical bodies. Colors, odors, tastes, feels, and sounds exist only as mental affects. Not only does Descartes's absolute mechanism exclude man from nature, but also everything not reducible to mathematical terms. Descartes's price of

principal seat in the brain, and it will be there like the fountain maker, who must be at the openings where all the pipes of these machines discharge themselves, if he wishes to start, to stop, or to change in any way their movements." (From "Descartes—Selections," ed. by Ralph M. Eaton; Chas. Scribner's Sons, New York, 1927. "Selections from the Treaties on Man." pp. 353–354).

[11] *Ibid.*, p. 354.

absolute mathematical certainty in science is a two-world theory with a radical discontinuity between extension and thought.

Descartes's absolute mechanism was rejected by both Boyle and Newton. Boyle was a vigorous advocate of the new mechanical or corpuscularian doctrine, but he was not willing to accept the complete mechanical determinism of Descartes. His own experimental inquiries were directed toward an explication of particular qualities by mechanical principles.[12] The "Corpuscular Hypothesis," for Boyle, is "the Hypothesis which teaches, that these Qualities depend upon certain contextures and other Mechanical Affections of the small parts of the bodies, that are indow'd with them, and consequently may be abolish'd when that necessary Modification is destroyed."[13] The "*Motion, Figure, Size, Posture, Rest, Order,* or *Texture*" of the material corpuscles suffice for the mechanical production of such qualities as heat and cold. The two grand principles of Natural Philosophy are Matter and Motion.[14]

Boyle's mechanism is a truncated version of Galileo's. The theory of mechanical principles and atomic properties is propounded without benefit of mathematics. Boyle's thesis is simply that local motion, size, shape, and contexture of physical bodies are the sensible and proper elements for the explication of qualities. They are to be

[12] *Cf.* "Experiments, Notes, &c. About the Mechanical Origine or Production of divers particular Qualities": By the Honourable Robert Boyle, Esq; Fellow of the R. Society. London, 1675. p. 7.

"For, I took upon me to demonstrate, that the Qualities of bodies *cannot* proceed from (what the Schools call) *Substantial* Forms, or from any other Causes but Mechanical, it might be reasonably enough expected, that my Argument should directly exclude them all. But since, in my Explications of Qualities, I pretend only, that they *may* be explicated by *Mechanical Principles,* without enquiring, whether they are explicable by any other; that which I need to prove, is not Mechanical Principles are the *necessary* and *onely* things whereby Qualities may be explain'd, but that probably they will be found *sufficient* for their explication."

[13] *Ibid.*, p. 10.

[14] "About the Excellency and Grounds of the Mechanical Hypothesis"; London, 1674. pp. 8–9.

preferred to the substantial forms and inherent qualities of the Aristotelians, and to "Hypostatical Substances," the Salt, Sulphur, and Mercury of the Chymists. The determination of amounts by measurement is generally missing from Boyle's experiments. This is not just neglect of such instruments as a thermometer, but failure on the part of Boyle to grasp the importance of measurement in Galileo's work and the need for quantitative results in his own field. His concern with the qualities of bodies rather than with mechanical laws of motion perhaps explains his neglect of mathematics. The atomic constitution of bodies and the sufficiency of mechanical principles to explain the production of qualities are the two main points of his corpuscularian theory. He is not willing, however, to subscribe to "the Contagious Boldness of some Baptiz'd Epicureans" who atheistically banish final causes from nature; nor to suppose, with Descartes, "the End of God in Things Corporeal to be so Sublime, that 'twere Presumption in Man to think his Reason can extend to Discover them."[15]

Boyle's objection to Descartes's supposition is based mainly upon his belief that plants and animals are not mere mechanical aggregates of material particles. He was impressed with the complexity of parts, the fitness of functions, and the interrelations of complexity and fitness in the living body. Such complexity, fitness, and contrivance seemed, as Boyle declared, "destinated to and for the welfare of the whole animal himself, as he is an entire and distinct System of organiz'd parts."[16] Purpose in living things is not due to any intention on the part of the things themselves. The design, however, may justly and commendably be attributed to God. Boyle's piety, though, does not get the better of his scientific discrimination. To advance from the uses of things to arguments about the Author of Nature is a metaphysical argument and Boyle so describes it. A physical argument

[15] "A Disquisition About Final Causes of Natural Things"; London, 1688. The Preface, A3–A4.

[16] *Ibid.*, p. 8.

dealing with the supposed purposes of things must be confined to the peculiar nature of the things themselves. And in any event, the naturalist worthy of the name must not let the search for final causes interfere with the search for mechanical explanations of qualities. " . . . the World being but, as it were, a great piece of Clock-work, the Naturalist as such, is but a Mechanitian; . . ."[17]

Boyle, in short, while not himself directly engaged in the development of the science of mechanics had come under the influence of mechanical ideas. His application of these ideas to chemical analysis was the forerunner of a host of similar attempts to extend mechanical concepts from the field of mechanics to other fields of physical investigation. He rejects Descartes's absolute mechanism on both empirical and religious grounds without taking account of the part played by mathematics in the Cartesian formulation. And, as has been pointed out, he also overlooked the mathematical method of measurement and demonstration in Galileo's "Two New Sciences."

Newton's position, in contrast to Descartes, involved the rejection of the claim of absolute certainty in science. This position, as Newton himself saw, follows from two traits of scientific inquiry. In the first place, the principles of science are inductive generalizations inferred from observation and experiments. "In experimental philosophy," Newton writes, "we are to look upon propositions collected by general induction from phenomena as accurately or very nearly true." Such very nearly true propositions are approximations which are not to be rejected unless found to disagree with the results of further experiments. They are always subject to revision and correction when confronted by additional or by adverse experimental evidence. In the second place, Newton, following Galileo, recognized the instrumental and methodological character of mathematics. Speaking of the solution of physical problems presented to the inves-

[17] "The Excellency of Theology Compar'd with Natural Philosophy": London, 1674. p. 169.

tigator of nature, Newton states that the solution of these problems is from mechanics and their demonstration is from geometry.

Therefore Geometry is founded in mechanical practice, and is nothing but that part of universal mechanics which accurately proposes and demonstrates the art of measuring. But since the manual arts are chiefly conversant in the moving of bodies, it comes to pass that Geometry is commonly referred to their magnitudes and Mechanics to their motions. In this sense, Rational Mechanics will be the science of motions resulting from any forces whatsoever and of the forces required to produce any motions, accurately proposed and demonstrated.[18]

Newton's chief objection to the Cartesian system of nature was directed against *a priori* mathematical constructions assumed independently of observation and experiment.

Newton hoped that the rest of the phenomena of nature would prove subject to the same kind of reasoning from mechanical principles which he had followed so successfully in his great work on "The Mathematical Principles of Natural Philosophy." This hope for a comprehensive mechanism was expressed as a hope and not as a dogma. Newton believed that mechanical hypotheses were the most plausible explications of phenomena. He was averse, nevertheless, to employing hypotheses as ultimate explanations. Their legitimate use should be to serve as queries leading to further experiments. In his "Opticks," he had ventured the mechanical hypothesis in which he supposed light to be composed of corporeal particles. When this hypothesis was attacked by Pardies and other critics, Newton pointed out that his empirical theory of light and colors drawn from experiments was not to be confused with what was offered only as a plausible supposition.

For the best and safest way of philosophizing seems to be, first to inquire diligently into the properties of things, and establishing these properties by experiments then proceed more slowly to hypotheses for the explanation of them. For hypotheses should be subservient only in explaining the proper-

[18] "The Mathematical Principles of Natural Philosophy." Sir Isaac Newton. Translated into English by Andrew Motte. Two Vols. London, 1729. Vol. 1, Author's *Preface*.

ties of things, but not assumed in determining them, unless so far as they may furnish experiments.[19]

A mechanical hypothesis offered as a general explication of phenomena does not have, for Newton, the same status as a theory or a principle inductively generalized from phenomena. The principles received by mathematicians, he asserts, should be confirmed by abundance of experiments. Only those qualities of bodies are to be held for universal which universally agree with experimental findings. Newton's empiricism was an effective ballast for the formal system of mathematical reasoning. The measures of motion determined by observation and the use of instruments, and the calculation of forces and the demonstration of propositions are both essential for mechanical science. Mechanical principles are born not from experimental philosophy alone nor from pure mathematics alone, but from their fruitful union in the science of Rational Mechanics. As Professor Blake has pointed out, Newton was not willing to acquiesce "in the Cartesian reduction of all the phenomena of nature to differing configurations of material particles possessing purely geometrical properties."[20]

The foregoing brief account of Newton's mechanism has tried to show the empirical and methodological caution with which he hedged in the doctrine of mechanical hypotheses and held to the reasoning from mechanical principles. The effect produced by Newton's work, however, was contrary to his own position. His followers, and they were many, enthroned the mathematical-mechanical system as the final word in scientific explana-

[19] "The Philosophical Transaction of the Royal Society of London"; Vol. VII, 1672, No. 85. (Abridged edition, p. 740.)

"To determine by experiments these, and such like quaeries, which involve the propounded theory, seems the most proper and direct way to conclusion. And therefore I could wish all objections were suspended, taken from hypothesis or any other head than these two: of showing the insufficiency of experiments to determine these quaeries, . . . or of producing other experiments which directly contradict me, if any such may seem to occur."

[20] *The Philosophical Review*, Vol. XLII, No. 5. Sept., 1933. Blake, Ralph M., "Sir Isaac Newton's Theory of Scientific Method." p. 476.

tion. They took the imposing structure of mathematical proofs and neglected the experimental and methodological conditions which Newton had been careful to point out. Newton's hope for a comprehensive mechanism became the enthusiastic dogma of the Newtonians. This dogma took the form of an assertion that the elements of mathematics in Newton's Fluxions were literally identical with the material constituents of nature.[21] What Newton had called the "mathematical way" was converted into a mathematical realism which assumed a complete correlation between mathematical and physical elements.

The attempt, after Newton, to establish mechanical principles in matters not hitherto subjected to quantitative analysis is to be noted in the *Transactions* of the Royal Society. The science of plant physiology was developed along mechanical lines in the "Vegetable Statics" of Stephen Hales. In contrast to this fortunate application and extension of mechanical ideas, one should note the unfortunate restrictions imposed by the dominance of the mechanical model in the conduct of scientific thought. The eighteenth century investigators of electrical phenomena, for example, were certain in their own minds that an explanation of the observed effects must fit within a mechanical framework and fall under known laws of statics and dynamics. Their minds were thus closed for a considerable time to alternative hypotheses. One should note, also, how the likeness of nature to a simple machine tended to confine and limit the concept of natural mechanisms. Galileo, as we have seen, derived his concept of the mechanism of nature by analogy from the operations of machines. The analysis of machines constituted the model for the analysis of physical structures

[21] Thus John Keill states, as one of the three principles to be laid down as the foundation of all physics, the purely mathematical postulate, "The divisibility of quantity in infinitum." Similarly, Edmund Halley assumes that the system of the world is "actually infinite" from the mathematical definition of infinity. Humphry Ditton, Charles Hayes, and other writers on Fluxions take the flowing quantities of Newton's calculus as "the very first Principles . . . of finite magnitudes." The shift is from geometrical analysis to what is "really and actually generated" in nature.

and processes. This "machine-ism" was given its sweeping, speculative generalization by Descartes, and its definitive scientific form in the work of Galileo and Newton. But from Galileo through Descartes and Boyle to Newton, the analogy remains the same. Nature is like a vast clock-work running by its own self-contained springs and exhibiting its parts and connexions for the measurements and demonstrations of the scientist. The concept of mechanism based on the model of a machine was triumphant in the seventeenth century; but, subsequently, mechanical ideas had to be liberated from a restricted adherence to the machine analogy.

The mechanism of the seventeenth century opposed the teleological, the occult, and the supernatural explanations of natural phenomena. It supplanted the anthropomorphic categories of a theological reading of nature by principles of physical operation. In the machine, the early-modern scientist found an analogy free from the vital interests and providential purposes which the medieval thinker located at large in the world and at home in God. For Thomas Aquinas, God was the Father of his creatures. For Descartes, God was the Master Mechanic of the world machine. The conception of the mechanical, based on empirical practice and discovery, was carried to speculative extremes by Descartes and some of the Newtonians in their pursuit of absolute mathematical certainty in science. Galileo and Newton, whose achievements in mathematical-physical science provided the main strength and support for the supremacy of the mechanical view, themselves restrained the tendency toward mathematical absolutism by never losing hold of the importance of experiment and observation. Their caution in scientific speculation in view of the greatness of their scientific achievements is a standing rebuke to those who are anxious for final answers in matters where men are never done with questioning.

THE SPECIES CONCEPT IN THE LIGHT OF CYTOLOGY AND GENETICS[1]

PROFESSOR R. RUGGLES GATES

KING'S COLLEGE, UNIVERSITY OF LONDON; DELEGATE FROM THE BRITISH ASSOCIATION AND THE AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE TO THE TWENTY-FIFTH (JUBILEE) SESSION OF THE INDIAN SCIENCE CONGRESS, CALCUTTA

ON the gene theory, variations arise for the most part in the chromosomes and express themselves in ontogenetic development, although cytoplasmic differences of an independent kind may also occur between species in certain genera, such as Oenothera and Epilobium (*cf.* Michaelis, 1937). An understanding of species and other categories of taxonomic classification must then ultimately be based mainly upon an analysis of how chromosomes change. This applies to all organisms except the lowest, such as the Bacteria and the Cyanophyceae, and in the latter group we may get some idea from recent work (see Spearing, 1937) of how the chromosome and gene mechanism may have arisen.

From the cytological point of view we may classify chromosome changes as changes (1) in number, (2) in structure. Changes in number include (a) polyploidy, so characteristic of plants, (b) polysomy, (c) fragmentation, (d) fusion of chromosomes. Structural changes include (a) segmental interchange, (b) duplication, (c) inversion, (d) deletion of a portion of a chromosome and (e) translocation between non-homologous chromosomes. Some of these changes involve no immediate phenotypic change in the organism, but they serve as a basis on which future differentiation of types can take place.

Comparative cytology throws light on the processes by which these changes in number have occurred. The study of chromosome structure combined with comparative genetics shows how rearrangements within the

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chromosomes have been taking place. Examples are the location of parallel mutations in the chromosomes of *Drosophila melanogaster, D. pseudo-obscura, D. virilis* and other species; or the catenation of chromosomes in different Oenothera species, and in certain other genera. The latter condition appears to have come about through segmental interchange accompanied by intercrossing. In all cases the ultimate raw material of evolution appears to be supplied mainly by genic mutations; but the existence of a position effect, which now appears to be proved, blurs the current conception of a gene as a definite body existing at one locus of a chromosome.

I have never accepted this conception of a gene, but as early as 1915 I pointed out that a gene really represents a *difference* which has arisen through a change or mutation at a position in a chromosome and is located by crossing-over experiments. Recent work on the salivary chromosomes of Drosophila has shown that some recessive mutations are really minute deletions or loss of a short portion of a chromosome, while some dominant mutations, *e.g.,* bar eye, are duplications of a few segments. In the study of gene mutations, as of other mutations, it is thus necessary to analyze the nature of the change which has occurred, and to recognize that genic changes of various kinds can take place. We shall thus arrive at a classification of gene mutations, just as chromosome mutations have already been classified (Gates, 1915a) through an analysis of the changes involved.

Goldschmidt (1937) has recalled the mutations pale and blond in Drosophila, in which chromatin rearrangements have taken place. He describes two new and striking cases, in one of which at least four "gene mutations" have appeared simultaneously at the left end of chromosome I; while in the other the three well-known mutations, dumpy, thoraxate and purple, as well as two others, all appeared in one brood as the result of a rearrangement within chromosome II. Such extensive rearrangements are admittedly rare and they require further analysis. Gold-

schmidt's conclusion that genes and gene mutations do not exist does not necessarily follow, if we accept the point of view that a gene is simply a difference arising in a chromosome. The fact that the *same* genic mutation occurs repeatedly, and even in different species, shows that the change which produces it is not a random one but must have some definite structural or chemical basis. The change in the basic chromosome number of a genus from 5 to 12 (in the Oryzeae), or from 7 to 13 (in Gossypium), or 7 to 17 (in the Pomoideae), represents one or more mutations of a still more fundamental character than the chromatin rearrangements mentioned above.

A recent paper of Sturtevant and Tan (1937) comparing the genes of *Drosophila melanogaster* and *D. pseudo-obscura* shows that these species have 54 parallel mutations, but the arrangement of the genes is quite different in the two species. Since they diverged from a common ancestor there have been fusions and interchanges and many rearrangements of genes within the arms of the chromosomes, including at least 19 inversions. A previous study of the salivary chromosomes in the sterile F_1 hybrids of *D. pseudo-obscura* and *D. miranda* (Dobzhansky and Tan, 1936) shows many translocations and still more inversions within the chromosomes. No sections of appreciable length were found to have the same disc patterns in the two species. There is already evidence that similar rearrangements have been at work in several other species, so that chromatin rearrangement has played an important part in the evolution of species in Drosophila. The study of mutation rates and their natural methods of change may ultimately throw some further light on the origin of this "raw material." Different genera of plants and animals have specialized in different methods by which the genes thus produced are rearranged, duplicated, multiplied or interlinked. In certain cases the evolution of a group of species may nevertheless advance on a common front by the selection of parallel mutations in species which have become intersterile. The problem of muta-

tions in relation to natural selection has been discussed elsewhere (Gates, 1936a).

Among the many striking cases of parallel mutations which have occurred in the modern work, reference may be made to two which appear to me to have special significance because the parallelism is in groups of animals as widely separated as insects and mammals. A strain of goats in Tennessee, some of which were afterwards bred in Texas, display the peculiarity (Lush, 1930) that when suddenly frightened their legs become rigid for ten to twenty seconds, so that they fall over. They gradually recover and will not react in this way again for about half an hour. This peculiarity of the nervous system is probably the result of a mutation, although the method of its inheritance does not appear to be determined with full certainty. The same condition has been seen in a flock of goats in Egypt. Now the "death-feigning" of insects appears to be the same sort of reaction, and I have long held the view that this habit in many insect species arose in the same way, through a single mutation.

That interpretation is strengthened by a recent case of parallel mutations in the nervous system of mice and Drosophila. Lord and Gates (1929) described a mutation of the house mouse known as "shaker," which is a simple Mendelian recessive in crosses. Lüers (1936) has recently described a mutation which he calls "shaker," which has occurred many times in the offspring of x-rayed *Drosophila funebris.* It is a simple, sex-linked dominant, not lethal, and the palsied symptoms are so similar to those of the mouse that while they may not be identical they show at any rate that the nervous system in these two very diverse phyla can undergo very similar mutations. Certain inherited forms of palsy in man are of course of a closely related type.

Very little is at present known about mutation rates. The subject has been discussed in relation to the human blood groups (Gates, 1936), but further reference may be made to it here. The modern work on mutations shows

that they occur repeatedly in any particular species with a frequency which varies widely but is characteristic of each mutation. The same mutation frequently occurs in related species, but obviously new types of mutations must begin to arise from time to time or there would be no differentiation of species and no evolution. Some mutations are probably as old as the species, in the sense that it has been producing these mutations from the time of its origin. Other mutations must begin to appear at different periods in the life of the species. The evidence of the blood groups in man, as well as recent evidence in Drosophila, indicates that a new mutation will not begin to appear simultaneously over the whole area occupied by the species, but rather that some local population will begin to produce this mutation with a certain frequency while over the rest of its area the mutation fails to appear.

If this mutation is advantageous to the species, then it is likely sooner or later to spread gradually through the whole species by natural selection, as Fisher (1930) has shown. Mutations such as the blood groups and probably many others, which are neutral as regards selection, will only spread according to their mutation rate, except in so far as they happen to be genetically linked to advantageous characters. The distribution of the blood groups in human races indicates that they do not belong to a selective linkage group, but that they are distributed wholly by heredity and the migration and crossing of races. Why mutation rates change, and whether they change gradually or suddenly, are questions which can not yet be answered; but the anthropological evidence leads me to conclude that, in some cases at any rate, the change is abrupt, a new mutation beginning to occur with ordinary frequency in a population in which it had not occurred previously at all. It is also probable that certain species which have been producing a particular mutation for a long period may ultimately cease to do so.

Various non-selective mutational characters may then be expected to arise in different parts of the distribution area of a species and to play an important part in differ-

entiating such a species into various sub-types or geographic races. The linkage of such mutations to other characters which are physiological and selective will account for the development in any species of local types which are adapted to their immediate conditions. Timoféeff-Ressovsky (1937) has shown that races of *Drosophila funebris* from (1) Western Europe, (2) the Mediterranean region, (3) Eastern Europe, Caucasus, Turkestan and Siberia, fall into separate groups which are physiologically adapted to the prevailing temperatures in their respective regions. His x-ray experiments with *D. melanogaster* indicate that small physiological mutations affecting the viability are among the most common mutations. In plants it appears that many at least of the differences found in local varieties are quite non-adaptive and occur indiscriminately in the same area, while others are physiologically adaptive. Various investigators have shown that wild populations of several different species of Drosophila in different countries are also heterozygous for many gene mutations.

Many interspecific crosses both in plants and animals show that their differentiation has arisen through genic mutation. The work of Baur (1932) on Antirrhinum showed that the thirteen species in Southern Europe and North Africa were differentiated by gene mutations, all having the same chromosome numbers and producing fertile hybrids which show Mendelian segregation. To take a case from animals, the breeding experiments of Sumner with Peromyscus justify the conclusion that many of the geographic sub-species in two different species are differentiated not by single but by numerous small genic differences. The indications are that these sub-species are species in the making, and that their differences are perhaps as numerous as the *specific* differences in Antirrhinum. That other changes take place in Peromyscus is shown by the fact that two sub-species of *P. maniculatus* differ in their chromosome number, *Gambeli* having 48 while *Hollesteri* has 52 (Cuénot, 1936). These two forms would probably show inter-sterility in crosses. This is one

of the types of cytological change which comes in to complicate the results of mutation by linking the genes into fresh groupings. Several other interesting cases of a similar kind are known in animals.

The various strains of *Drosophila melanogaster* with united X-chromosomes in the female are well known, and there is evidence that a similar condition may occur in certain human pedigrees. Matthey (quoted by Cuénot, 1936) found that male lizards of the species *Gerrhonotus scincicauda* in the same locality in Switzerland all had 24 microchromosomes, but that some individuals possessed 21 macrochromosomes (one of them V-shaped) while others had 20 macrochromosomes (two of them V-shaped). Evidently in the latter a second pair of rod-shaped chromosomes had united to form a V. Swezy (1928) studied the chromosome numbers in a mixed colony of rats begun in 1910 by crossing the Wistar white rat with the wild gray rat. Of 50 rats examined, 27 had 42 chromosomes and 23 had 62 chromosomes. The origin of this dimorphism was traced to the wild gray rat, four individuals of which had 42 diploid but 21 and 31 haploid chromosomes. According to Cuénot (1936, p. 215), guinea-pigs also show two chromosome numbers, $n = 19$ and $n = 30$. Lancefield (1929) described two "physiological species" of *Drosophila obscura* from Western North America which were identical in appearance but differed in the Y-chromosome of the males, which was a rod in one and a (longer) V in the other. Intercrossing is difficult because females of one race frequently refuse to accept males of the other race. In crosses, the F_1 males were sterile, and the offspring of F_1 females showed deviations from the normal sex-ratio as well as reduction of crossing-over in parts of the X-chromosome. Evidently rearrangements had taken place within the X- and Y-chromosomes of these two strains, resulting in failure to interbreed and making them the starting point for two new species.

It was supposed until recently that interspecific sterility could only arise gradually over a long period and that it represented the final stage in the production of a true

species. Recent experimental work has not only resulted in the immediate production of new species with all the criteria, including those of intersterility and change in chromosome number, but has shown, as in some of the cases cited above, that intersterility is frequently the first stage rather than the last in the production of a new species. A rearrangement of portions of the genome—an internal change which may have no phenotypic effect—has often occurred in one strain of a species, making it more or less infertile with the type. As a result of this intersterility the new type, as a fresh center of breeding and mutations, is placed on the road to becoming a new species.

The conceptions associated with the terms linneons, jordanons and syngameons have proved most useful in the genetic analysis of species and their variations. One may perhaps classify all the possible criteria of a Linnean species or linneon. It will be distinguished from its neighbors (a) morphologically, in its phenotype and its chromosome number or their morphology; (b) by physiological and chemical differences, including intersterility; (c) ecologically and in geographical distribution. Not all linneons need answer all these requirements. For instance, several may agree in chromosome morphology, in ecological habitat and in geographical distribution. In the practical work of describing and dealing with species the only essential, however, is a sufficient number of morphological differences. To these, any or all the other kinds of difference may be added.

It was supposed until recently that interspecific sterility could only arise over a long period and had never occurred in experiment. Some biologists still regard intersterility as an essential criterion of species. However, when we remember the extensive phenomena of self-sterility and the many other forms of sterility which exist, it is clear that intersterility is no longer a sure guide even regarding nearness of relationship between types.

As late as 1922, Bateson was able to say, "that particular and essential bit of the theory of evolution which is

concerned with the origin and nature of *species* remains utterly mysterious." . . . "Variation of many kinds, often considerable, we daily witness, but no origin of species." . . . "The production of an indubitably sterile hybrid from completely fertile parents which have arisen under critical observation from a single common origin is the event for which we wait." In the fifteen years which have elapsed since that striking utterance, these conditions have been amply fulfilled in all essentials. The origin of interspecific sterility is no longer the mystery it then seemed. The difficulty was overstated even in 1922. Polyploid and aneuploid mutations were already well known to be partially sterile with their parent form; and such tetraploid mutations as *Oenothera gigas*, differing from the parent species not only in morphological characters and in pollen form but also in physiology, were recognized by many as in all essentials new species. Nevertheless, the production of amphidiploids, of which some two score are now known, from interspecific and even intergeneric crosses, marked a new departure and clearly fulfils every criterion that could be asked for in a new species.

It is now evident that the causes of interspecific sterility are much more definite and various than was formerly supposed. They arise from a variety of kinds of change in the chromosomes and even in the cytoplasm.

The term species is clearly impossible to define, because they have arisen in many ways and there is no sharp line of demarcation between species, sub-species, variety and jordanon. The very nature of species varies from group to group, depending on the prevalent kinds of variation, and is quite different in practice in say flowering plants, the lower algae and bacteria.

The Onagra section of the genus Oenothera, a group of interfertile Linnean species numbering over 75, is a good example of a syngameon. In this genus chromosome catenation and small, self-pollinating flowers have evolved simultaneously. Under these conditions the seeds from each individual produce a pure line, although the species is persistently heterozygous. Catenation preserves the

advantages of heterosis. Occasional crosses occur naturally when dispersal brings different members of the syngameon into contact, thus producing new types which again breed true. This behavior combined with gene mutations results in a network of cross-related forms, linneons, jordanons and many smaller differences.

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DURING WHICH STAGE IN THE NUCLEAR CYCLE DO THE GENES PRODUCE THEIR EFFECTS IN THE CYTOPLASM?[1]

PROFESSOR CURT STERN
DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ROCHESTER

CONSIDERING the importance generally agreed upon by biologists as to the rôle of the nucleus in the life processes of cells, our actual knowledge of its interaction with the cytoplasm is very limited. Even the highly developed theory of the gene, which places the hereditary determiners of the most diverse and fundamental biological phenomena within the nucleus, does not indicate how the products of gene activity in the nucleus find their way into the cytoplasm of the cell. Two main possibilities for this transfer are apparent. Either the cytoplasm is acted upon during the "resting" or "energic" (Berrill and Huskins, 1936) state of the nucleus or the unknown substances produced inside the nucleus are released into the cytoplasm when the nuclear membrane breaks down in preparation for division. Whether, in case of the first alternative, one should think of the nuclear membrane as permeable for end products of genic reactions or whether one should assume a direct gene-cytoplasm interaction at the nuclear-cytoplasmatic interphase will not be discussed here. It is possible in the third place that the mitotic stage represents a period of special gene activity during which time determining substances are not only released but actually produced. As there are no facts available which support this view, we shall not consider it further. It should be added that the interaction between gene and cytoplasm may also be of the type "extraction of substances from the cytoplasm into the nucleus" instead of "release from the nucleus into the cytoplasm." The following discussion can easily be adjusted to this view.

[1] Contribution No. 194 from the entomological laboratory of the University of Illinois.

General considerations of the different fate of nucleated and enucleated cell-fragments and the changes observed in non-dividing nuclei which coincide partly with certain cytoplasmatic processes (*e.g.,* in active and non-active periods of secretory cells) have led many geneticists to the assumption of the first alternative, that of genic effects during the energic state. But none of these observations is concerned with specific effects whose genic nature is proved. On the other hand, discharge of nuclear material into the cytoplasm as observed in many eggs during the breakdown of the membrane of the germinal vesicle has led some authors to the belief that nuclear division in general provides for the release of gene products.

These arguments are not beyond doubt. Moreover, it seems possible that interaction during the energic state as well as release of substances during disappearance of the nuclear membrane play a rôle in the nuclear cytoplasmatic interrelations. The purpose of this note is to point out a method of attack on this problem and to show to what result the interpretation of certain data leads. It should be added that the reasoning to be presented has already been used implicity in various genetic analyses without a critical evaluation of its basis.

If the genetic constitution of a cell is changed and if a cytoplasmatic effect of the new genetic constitution becomes apparent in this single cell before nuclear division has occurred then it is obvious that the gene concerned has interacted with the cytoplasm during the energic state of the nucleus. If on the other hand the cytoplasmatic effect of a changed genetic constitution becomes visible only after nuclear division and in the two ensuing daughter cells then the conclusion is suggested that the disappearance of the nuclear membrane is necessary for the release of the gene-dependent substances. However, the latter assumption is warranted only if it can be shown that there has been sufficient time for the new genetic constitution to produce an effect before the nucleus divides, or

that the cellular changes coinciding with division are not necessary for the visible expression of the genic products which may already have passed the nuclear membrane. It may be difficult to exclude these possibilities. Thus it is apparent that it will be easier to draw conclusions in case of immediately visible effects than in case of "delayed" ones.

Such changes in genetic constitutions occur in somatic tissues as the result of mutations or of chromosomal processes like segregation, non-disjunction, etc.; and in germ cells as the result of recombination of genes during the maturation divisions. Strictly speaking, most of these changes relate to a comparison of the constitution of a daughter cell with its mother cell. Furthermore, as a cell with the gene "a," derived from a mother cell "Aa," acquires its constitution at the anaphase of the segregating division, it could be supposed that "a" produces its effect before the new nuclear membrane has been formed at the telophase. However, as pointed out before, it is assumed that the condensed mitotic stage of the chromosomal material does not constitute a period of gene activity. Should this assumption be proven wrong, the arguments presented in this paper will obviously lose their weight.

There are not many cases in which genetically determined characters can be observed in single cells, and of these only very few contribute information to our problem. A search through the literature has yielded the following, exclusively in plants:

Mutation or segregation in somatic cells: In the higher plant *Delphinium ajacis,* so-called unstable genes have been described by Demerec (1931). While the original constitution of the cells of the petals gives rise to light pink cytoplasm, cells containing the "mutated" gene possess a purple anthocyan. The number of cells involved in a spot, according to Demerec, falls well into the series 1, 2, 4, 8, ..., 2^n, indicating the number of cell generations

which have passed since the original "mutant" cell was produced. The presence of one-cell spots, in numbers equivalent to those of multicellular spots, proves the ability of the "mutated" gene to interact with the cytoplasm during the energic nuclear stage.

A similar case in corn has been found by Dr. D. F. Jones, who has kindly permitted me to quote from his forthcoming paper. Endosperm of the constitution ccC is medium colored. Twin spots of light and dark coloration occur frequently, presumably of the constitutions ccc and cCC due to somatic segregation. Some of these twin mosaics include only one cell in each area. If these cells possess only one nucleus, a fact not yet established, then the new constitutions which the segregating divisions produced in the two daughter cells were able to interact with the cytoplasm despite the continuous presence of a nuclear membrane.

Segregation as a result of the reduction division: There are some factors which are expressed in the "gones," *i.e.*, the immediate products of the meiotic divisions. When the *first* division is reductional for a pair Aa and when a cell wall separates the two nuclei resulting from it, two cells are formed with the constitution A and a, respectively. The second division results in four cells, two with

TABLE I

		Reduction at first division		Proportion of phenotypes	Reduction at second division		Proportion of phenotypes
Gonocyte I		AAaa			AAaa		
Gonocytes II		AA	aa		Aa	Aa	
Gones		A A	a a		A a	A a	
Phenotype of gones if determined	1. during division	both A	both a	2A : 2a	both A	both A	4A : 0a
	2. during energic state	both A	both a	2A : 2a	A a	A a	2A : 2a

the factorial constitution A and two with a. Regardless of the determination of the gonic phenotype either during the second division or directly through the energic state

of the gonic nuclei, the daughter cells of the secondary gonocyte A will both be phenotypically A and those of the secondary gonocyte a will both be a. On the other hand, if the factorial segregation occurs during the *second* meiotic division, both secondary gonocytes will be of the constitution Aa. In this case two different groups of two gones each should appear only if their phenotype is conditioned by the constitution of their own nuclei, while all four gones should be alike if determined during the second division by the constitution of the secondary gonocytes. These considerations provide us with a potential criterion, since it is known that reduction in respect to a given locus occurs at the first division in some gonocytes and at the second in others wherever crossing-over takes place at the four-strand stage. Consequently, as reduction at the first division results always in equal numbers of the two gonic phenotypes, while reduction at the second division results in two phenotypes only if the genic-cytoplasmatic interaction of the gones occurs during the energic state, a finding of phenotypically visible segregation in *all* gonic tetrads constitutes evidence for the latter alternative (Table I).

At present there are no data available from the higher plants which permit a sufficient analysis of genetically determined characters of gonic *tetrads,* but we possess observations on dimorphism of *large samples* of pollen. Such observations could theoretically be utilized for our problem, whenever the gene in question is segregated in some gonocytes at the first and in others at the second division. As seen above, visible segregation in all gonic tetrads constitutes evidence for interaction during the energic state and such segregation should express itself in numerical equality of the two types even in a population of gones. However, the observations of pollen dimorphism with regard to properties of reserve carbohydrates in corn (Demerec, 1924, Brink and McGillivray, 1924, Longley, 1924) can not be used for the present dis-

cussion. Though the two kinds of pollen grains are found in equal numbers, no conclusion is justified, as the gene responsible for the difference probably is segregated always at the first division. Moreover, the differential staining reaction can not be observed till several days after the first nuclear division in the pollen grains. Probably the situation is similar in regard to time of appearance of the phenotype in the case of pollen dimorphism in rice (Parnell, 1921). Here, then, we deal with data in which further work should clear up the question of whether the gametophytic division is necessary for the appearance of the specific carbohydrate or whether these are examples of cytoplasmic processes dependent on interaction during the energic state but requiring a comparatively long period for their visible expression.

A somewhat similar problem is raised by the well-known case of long *vs.* round pollen grains in *Lathyrus odoratus,* where only one kind, namely, long pollen is formed by a heterozygotic plant. Thus the genotype "round" of half the pollen grains is unable to express itself visibly. For an explanation of this fact one must consider the relatively late appearance of a cell wall separating the four gonic nuclei of a pollen mother cell in Lathyrus and the possibility of a very early cytoplasmatic predetermination of pollen shape as well as the points considered above.

In lower plants observations on different species of the smut fungus Ustilago and of the green flagellate Chlamydomonas are relevant for our discussion. Here the four gones belonging to one tetrad were analyzed with reference to visible characteristics.

In Ustilago (Hüttig, 1931) the germinating diploid brand spore forms a promycelium consisting of four haploid cells which result from two meiotic divisions. If we number these cells 1, 2, 3 and 4 in order of their arrangement in the cell filament, it has been shown that 1 and 2 and respectively 3 and 4 are sister cells derived from the second division. Under appropriate conditions these cells

can be made to copulate among each other. In many cases the sexual reactions occur between two sister cells. These reactions are proof of sexual differences of the copulating cells which are dependent upon two alleles, A and a. In cases of sister cell copulations the second division of the promycelium has been reductional, giving the alternative constitutions A and a to the two sister cells. The genes A and a then are able to exert their sexually differentiating effect during the energic nuclear state.

Crosses between different forms of the haploid flagellate Chlamydomonas yield zygotes which undergo two meiotic divisions leading to the appearance of four new haploid individuals. Apart from zygotes which produced only two types of gones Pascher (1916, 1918) refers to one case where each of the four gones was different from the other three with respect to various morphological characteristics. Although a detailed genetic analysis is lacking it appears that the second meiotic division was reductional at least for certain genetic factors which are able to interact with the cytoplasm during the energic nuclear state.

An experimental attempt to change the genetic constitution of a cell and to observe the effect has been made by Hämmerling (1934). He exchanged the nucleus of the marine alga, *Acetabularia mediterranea,* for that of the related species, *A. wettsteinii,* and observed effects of the resting nucleus. However, this case does not fall completely within our discussion, as it was impossible to transplant the nucleus without a comparatively large amount of cytoplasm.

Conclusion: In the more decisive cases we have seen that specific genes can interact with the cytoplasm during the energic state of the nucleus. These genes are concerned in the production of anthocyans, of specific sexual reactions and of different morphological characteristics. Further work undoubtedly will increase the number of known cases. It remains to be seen whether

examples will be found in which gene-controlled substances exert visible effects after the breakdown of the membrane only, as is possible in some examples of pollen dimorphism. The interpretation of such cases involves difficulties which have been pointed out.

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THE RISE OF ENTOMOPHAGY AMONG LEPIDOPTERA

PROFESSOR W. V. BALDUF
UNIVERSITY OF ILLINOIS

ATTEMPTS at solving such a theoretical problem as the origin and development of a particular habit are more likely to yield sound conclusions in the case of orders, such as the Lepidoptera, whose larval food practices are characterized by a considerable diversity than would be possible in groups whose larvae are limited to a single mode of feeding. The value of diversity lies in the belief that one food habit within a group was derived from another existing in the same group and that the several types of feeding correlate more or less with the bodily structures, which have arisen by genetic mutations. In the present order occur not only the predominating plant-eating type of caterpillar, but also entomophagous, scavengerous, cannibalistic and homophonous forms. The latter embraces such as kill yet do not ingest others of their kind. Moreover, the food relations of the phytophagous majority range from leaf-eating and leaf-mining to boring in the stems, feeding at the roots, infesting flowers and seeds, and living at the expense of lichens and algae that frequent other plants. However, not all these relations between plants and caterpillars have a bearing on the question of origins in the case of entomophagy. But the cortex- and lichen-eating forms in particular fall under consideration here because they exhibit the antecedent habits from which most types of entomophagy seem to have sprung. Entomophagy among caterpillars is here regarded as constituting four types—cannibalism, occasional predatism, habitual predatism and parasitism.

CANNIBALISM

Cannibals are those which subsist in part on the living bodily tissues of their own kind. Cannibalism among

caterpillars, as elsewhere, is therefore never absolute but merely an occasional diversion from their prevailing habit of ingesting fresh plant tissue. Cannibalistic caterpillars have been known to make use of either the egg, larva or chrysalis of their own kind. While this food relation is said to obtain in nature it has been reported mostly for captive species and generally seems to result from hunger and thirst, which are, in turn, traceable to neglect by the captor. Accordingly, and as expected, this form of entomophagy is not confined to any taxonomic group but may presumably exhibit itself in almost any species held captive without a proper quantity or kind of food. Instances of cannibalism have been reported for the butterfly families Papilionidae, Danaidae, Pieridae and Lycaenidae, and the moth families Sesiidae, Sphingidae, Notodontidae, Lasiocampidae, Arctiidae, Syntomidae, Cossidae, Hepialidae, Noctuidae, Geometridae, Pyralidae, Tortricidae, Talaeporidae and Pterophoridae. The Noctuidae lead all others by far in the number of known cannibalistic species, while the Geometridae and Arctiidae rank second and third, respectively. Considering that the phenomenon is incidental in character, it will perhaps be found to correlate in its extent with size of family and the number of observations made under artificial conditions.

Occasional Predatism

This type of caterpillar embraces two subtypes, the first of which consists principally of phytophagous species, the second largely of scavengerous forms. Subtype one is very similar to the cannibalistic type of entomophagy in its bionomic features. Whereas cannibals limit their attack to other individuals of their own kind, this subtype of occasional predator chooses insects beyond its own species when it sometimes turns predacious. Their victims are insects, or perhaps other small animals, that chance to share the same cage or occur in their vicinity when hunger or thirst impel the caterpillar to deviate thus

from its normal plant-eating habit. Accordingly, these occasional predators and cannibals differ essentially only in the taxonomic relationship the victim or prey sustains to the offending species. Moreover, occasional predatism, like cannibalism, seems to be but a chance outgrowth of unsuitable or inadequate food supply. Most of the known examples belong to the families named above as having cannibalistic species.

The other subtype of occasional predatism is exemplified by several Pyralidae, which seem to be predominantly scavengerous but sometimes prey on other living insects. For example, a species of *Ephestia* is primarily a scavenger but at times devours the larvae and pupae of *Eublemma* and *Holcocera,* small moths that share its habitat and compete for the same food supply, which is the lac scale, *Tachardia lacca.* This subtype therefore seems to arise from the juxtaposition of the sometimes predacious insect to other insect life and waste organic matter.

PARASITISM AND HABITUAL PREDATISM

Parasitic and habitually predacious caterpillars differ from cannibals and occasional predators in electing to feed, with few exceptions, exclusively on the bodies of other living insects and in never reverting to phytophagy in an occasional way. Regarded from the standpoint of the inception of their entomophagy, habitual predators constitute two very distinct groups. The first is characterized by the fact that almost all its representatives utilize Homoptera as prey and may therefore be designated the *homopterophagous group.* The known examples are contained in the families Noctuidae, Heliodinidae, Tortricidae, Cosmopterygidae, Blastobasidae, Pyralidae and Lycaenidae. The second group is comparatively very small, containing only a few species, all of which are Lycaenidae and differ bionomically from the homopterophags in being phytophagous during their earlier instars and predacious in the later stadia. Ac-

cordingly, these may be named *phyto-predators*. The parasitic Lepidoptera constitute a somewhat distinct habit division and will therefore be treated separately below.

A general summary of the known bionomics of the homopterophagous and phyto-predatory groups is essential here to provide the factual basis for the theories advanced below to account for the origin and rise of their food habits.

The Homopterophagous Group

It is an impressive fact that all homopterophagous Noctuidae belong to the subfamily Erastriinae. Moreover, all the predatory members of this subfamily of comparatively small forms prey exclusively on Coccidae or scale insects. The species fall into the genera *Erastria, Thalpochares, Selepta, Catoblemma* and *Eublemma*. In their relations with Coccidae, the caterpillars enter the victim by burrowing into its waxy or resinous cover. They remain hidden either beneath a portable shelter constructed of debris or build a fixed covered runway. In one of these ways, the larvae move from one scale to another without exposing themselves to view. The larvae of *Eublemma amabilis* Moore and its congeners bore into the resinous encrustation secreted by the Indian lac scale to spend the entire stage. All coccidivorous Erastriinae also pupate within these shelters. The homopterophagous Heliodiniae, Cosmopterygidae, Tortricidae, Blastobasidae and Pyralidae resemble the Erastriinae in being tiny as larvae, in developing exclusively at the expense of Coccidae and in living under cover of the prey insects or beneath a special shelter fashioned from organic debris.

The Lycaenidae differ from the other homopterophagous groups just described in that they feed upon several other families of Homoptera in addition to the Coccidae. Moreover, *Liphyra brassolis* Westw. has been reported to go so far as to prey upon the larvae of ants. Several extremely remarkable interrelations have been found to exist between the small larvae of these butter-

flies, various species of ants and the homopterous inquilines of ants. A thorough study of the mass of data assembled by the writer from numerous published articles concerning phytophagous and predacious Lycaenidae alike makes it quite clear that these surprising conditions are essentially the consequences of two types of structure borne by the caterpillars.

Glanduliferous Lycaenidae

The larvae of many species bear a honey gland on the dorsum of the tenth bodily segment and a pair of eversible tubes on the eleventh. This group may, for convenience in reference, be called the glanduliferous type. The honey gland emits a somewhat viscous and clear fluid. Observations by a number of scientists indicate that the secretion is usually exceedingly palatable to ants. As a consequence, ants commonly gather about and upon the small larvae and stroke the organ with their antennae to induce the emission of the honey fluid. But the secretion is often also produced voluntarily by the larva in the absence of ants. As a consequence of the attractiveness of the glandular product, certain ants are known to direct the larvae to their nests to spend the night or day or to pupate. In all such cases, the relation between ant and larva is friendly—a mutualism that provides the larva protection, and sometimes shelter, transportation and even food, while the ant derives a delectable confection as its part.

Glandless Lycaenidae

The larvae of many other species are reported positively to lack these ant organs. Despite the absence of ant organs and their attractive product, caterpillar and ant have established an interrelationship that is beneficial to both. While the attitude of the ant is cool or hostile, fatalities to the lycaenid are usually avoided by virtue of the protected nature of the caterpillar. Immunity is secured either through various types of hairy or spiny vestiture or the possession of a tough carapace-like exo-

skeleton which may be lowered to the support on all sides when ants seek to attack the vulnerable ventral surfaces of the body. On the other hand, the two conflicting organisms are drawn together by their mutual interest in a third insect, which is invariably some member of the order Homoptera. To date, species of the families Coccidae, Fulgoridae, Cicadellidae and Aphidae have constituted the third corner of this triangular biological complex. The capacity of all the homopterous species reported in such relationships to yield an anal excretion known as honeydew readily explains the interest exhibited by ants in them. The caterpillar, however, is no less attracted to the same Homoptera but rather by its appetite for their tender juicy bodies or, in one instance, their fluid anal excretions. Moreover, when the triangle makes the nest of the ant member its habitat, the caterpillar may actually be fed orally by the ants in the same manner that they feed their own young, while the caterpillar of another species goes so far as to devour the young of the host ant itself.

The composite picture presented by the glanduliferous and the glandless types of Lycaenidae may perhaps be clarified somewhat by the following synopsis of ant—lycaenid—Homoptera interrelations. In it the species are grouped first according to their food habits and second by their relations with ants, which relations are in turn determined by the possession or lack of ant organs or the occurrence of various types of protective vestiture or body surface. Because the evolution of the entomophagy of these homopterophagous Lycaenidae seems to be traceable to an earlier phytophagous mode of life, species of all food groups are included in this synopsis.

I. Phytophagous Lycaenidae. Groups A to C are myrmecophilous, whereas D and E are amyrmecophilous.

A. Larva has the special ant organs and is attended by, but not dependent on ants. This division embraces the majority of the Lycaenidae that can be allocated to-day on a bionomic basis. It embraces species from the Theclinae, Chrysophaninae and Lycaeninae.

B. Larva has the special ant organs and is attended by, and dependent on ants. The known examples are Lycaeninae, Ogyrinae and Chrysophaninae.

C. Larva possesses no localized ant organs in the form of a dorsomedian gland and eversible tubes but is nevertheless thought to yield a secretion that may prove to emanate from numerous minute hypodermal glands. The larva is attended by ants but is not dependent on them. The best-known example is *Chrysophanus dispar rutilis* Wernb.

D. Larva has no ant gland but modified eversible tubes, and is not attended by ants. The modified tubes are said to function to drive ants away. *Curetis thetis* Dr. and *C. malayica* Feld. are the known examples.

E. Larva possesses no kind of ant organ, and is disregarded by ants. Species from the Lipteninae, Ogyrinae, Theclinae and Lycaeninae exemplify this condition. The larvae of the Lipteninae are hairy like those of Lymantriidae.

II. Phyto-predaceous Lycaenidae. The larvae feed on aerial parts of plants during the earlier instars, but in the later stadia inhabit the nests of ants whose brood they devour. Both gland and tubes are present and function particularly in the later instars. The species of this class are exclusively members of the genus *Lycaena sensu latu,* and European.

III. Homopterophagous Lycaenidae. Ants are either friendly or hostile to the larva; special ant organs present or lacking; larva sometimes protected by vestiture, texture or form of body wall or by its hidden position among the prey species.

A. Amyrmecophilous Homopterophags. The four genera known to exemplify this combination of bionomic characters are *Aslauga, Spalgis, Feniseca* and *Megalopalpus.* The first is liptenine, the rest lycaenine. The larvae lack ant organs and are bodily protected against ants.

B. Myrmecophilous Homopterophags. This type is exemplified by *Gerydus,* Gerydinae, and *Triclema,* Lycaeninae. The larvae yield a substance attractive to ants and are consequently treated in a friendly way by the latter.

IV. Myrmecophagous Lycaenidae. Larva perhaps lacks the special ant organs, lives in nests of a tree ant, and has a body protected against its hosts. *Liphyra brassolis* Westw., Liphyrinae, is the only species that is known to embody these characteristics.

V. Homopterophagous-excretophagous Lycaenidae. Larva lacks the special ant organs but is at once associated with and protected against ants. The lycaenine, *Lachnocnema bibulus* Fabr. is the only example known for this class.

VI. Excretophagous Lycaenidae. Larva lacks the special ant organs but lives with and is also protected against ants which feed it orally as they do their own larvae. *Euliphyra mirifica* Holl. is the sole representative recorded for this class of myrmecophiles.

Origin and Rise of Habitual Predatism

It has already been stated that habitual predatism seems to have had two separate origins and consequently

evolved independently in two different directions, giving rise to two bionomic groups described above as homopterophagous and phyto-predacious, respectively.

The homopterophagous series, which embraces representatives of several families of moths in addition to some Lycaenidae, is here regarded as representing the culmination of a number of modifications from an earlier phytophagous food habit. However, the evidences in support of this theory are most convincing in the Lycaenidae in particular because its genera and species still exhibit a number of distinct habit types that presumably represent the several levels traversed by the family in its evolutionary history.

Lichenivora

In the series of developmental steps leading to the homopterophagous group the lowest seems to be represented by certain species of *Iridana, Teratoneura* and *Epitola*—African genera of the subfamily Lipteninae. The larvae are clothed with hairs and possess unpaired dorso-median abdominal organs which seem to yield no secretion attractive to ants and are probably not homologous with those known in the higher Lycaenidae. Both the vestiture and the organs recall the caterpillars of the Lymantriidae. While ants may appear in the vicinity of the larvae their attitude is one of disregard that is thought to be traceable to the hairy coat of the caterpillar. The larvae feed on lichens infesting the trunks of trees. On account of this habit and their lymantriid-like structures, these genera are believed to represent the earliest surviving bionomic level of the family.

Homopterophaga

The habit group that throws most light on the origin of habitual predatism is composed of the coccidivorous genera *Spalgis, Feniseca, Triclema* and *Aslauga,* but *Aslauga* is the most significant of them because it is related to the lichenivorous Lipteninae of Africa. Their

taxonomic connection indicate they have had a common genetic background despite the present discrepancy in their food habits. When we compare the phytophagism of the lichen-eating genera with the coccidivory of *Aslauga* there proves to be but little essential difference between the two food practices. While belonging to two distinct kingdoms of organisms, lichens and coccids are alike as food for caterpillars in being minute, sessile creatures with similar bodily texture. These physical features enable the caterpillar to obtain either organism with ease and to ingest one as readily as the other. Moreover, both food organisms live exposed on the surface of trees and may presumably occur intermingled simultaneously on the same individual plant. Accordingly, the lichen and the coccid may be ingested interchangeably or even at the same time. But should conditions arise, as they doubtlessly not infrequently do in nature, which do not favor the growth of lichens, the caterpillar finds itself confronted with a choice between starvation or subsisting on Coccidae alone. Having eaten lichens and Coccidae promiscuously in its earlier generations or history, the species is now equipped with sufficient gustatory flexibility to permit it to flourish on an absolute diet of scale insects. Should the lichens continue to lack for a period of years, the casual predator may become a confirmed coccid-eater. The change from phytophagy to coccidophagy was therefore, according to this theory, accomplished in consequence of a change in the food supply available, the innate or acquired flexibility in the taste range of the larva, similarity in the physical and ecological characteristics of lichens and scale insects, and the ability of the larva to derive the necessary sustenance from either kind of food organism.

The case of *Aslauga* presumably falls into the glandless group of Lycaenidae, but another instance, that is equally convincing for this theory of origin of coccidiphagy, is at hand in the gland-bearing lycaenine genus *Triclema*. Rather limited observations show that the larvae of *T.*

lucretilis Hew. ate the young cortex of a plant, which bore Coccidae also, whereas those of *T. lamias* Hew. actually preyed on a *Lecanium* infesting twigs of *Imbricaria.* Being congeneric, it may be accepted without question that these species of *Triclema* had a common and not so far distant genetic history. Since they doubtlessly possess very similar mouthparts, the caterpillars of the two species are capable of ingesting with equal readiness food materials that, while they belong to widely different taxonomic groups, yet are similar in their general physical and nutritional characteristics. This theory of the derivation of the coccidivorous practice from a cortex- or lichen-eating ancestry may perhaps be advanced with equal validity for the genera *Spalgis* and *Feniseca,* which live among and prey upon Coccidae of the mealybug type that infest plant surfaces in masses.

The history of evolution in the food habits of the other, or moth families of homopterophagous Lepidoptera can not be traced step by step owing to the lack of contemporary related representatives to exemplify the several developmental grades. However, it is doubtlessly significant that all the insects selected by them as prey are Coccidae. Certainly the confinement of their choice to these minute, sessile, bark-inhabiting and least resistant members of the insect class could not have been a mere coincidence. Rather it seems clear that these larvae, which are uniformly small, had fed upon the cortical layer of plants or on lichens occupying plant surfaces before they adopted these Coccidae as food just as the present-day coccidivorous species of *Aslauga* had ancestors that were lichenivorous in habit.

The level on which the above moth groups stand constitutes the lowest represented among the homopterophagous series. They find the prey insects in their original habitat on exposed plant surfaces, visit them to devour their bodies directly and maintain a simple bilateral relation with them. Higher grades of predatism are to be found only in the Lycaenidae. As already pointed out, these

higher developments have been possible only because the larvae possess either the dorso-median honey gland and the pair of eversible tubes or some sort of protective vestiture or a carapace-like covering. By virtue of the gland, whose secretion inhibits the normal tendency of ants to destroy the otherwise defenseless caterpillars, or the vestiture features that render the body invulnerable, these lycaenid larvae have succeeded not only in living in intimate association with ants but also in establishing a variety of more or less complex relations with them and their homopterous guests. That all such involvements with ants and their inquilines have grown out of an earlier coccidivory seems to be indicated by certain bionomic features exhibited by *Aslauga* that have remained unmentioned up to this point. A brief account of this genus will reveal the foundations for this belief.

Aslauga caterpillars live on the bark of trees in the midst of Coccidae of the genera *Dactylopius, Lecanium* and *Stictococcus* and prey upon them. Tree ants of the species *Cremastogaster buchneri* attend the same Coccidae to secure their honeydew. Thus, actuated by their common need of food, the ant and the caterpillar are drawn together into close geographical proximity, yet maintain an attitude of mutual respect owing to the protective coat of the lycaenid. The ant frequently covers its coccid protégés with a layer of debris which may later be extended to form more or less permanent nests. Because the caterpillar resides among the Coccidae, it becomes incorporated within the ants' nest. Such inclusion is, therefore, a result of chance and not an expression of regard on the part of the ant. The two species are, in fact, competitors for a common source of food, and the caterpillar repays the ant with no useful substance or service in return for the shelter acquired. It seems quite clear then that while *Aslauga* demonstrates how predatism arose from the lichenivorous habit, it also illustrates the procedure by which the later and more complex triangular intranidal interrelations involving ants, lycaenid caterpillars and

Homoptera grew out of the earlier extranidal bilateral type of relation between ant and caterpillar that still predominates in this family.

Another and distinctly different manner of achieving the intranidalism of lycaenid larvae is exhibited in the instance of *Gerydus boisduvali* Moore. This Javanese caterpillar lives a free life on trees, where it preys on Coccidae and Aphididae. So far as this predatism is concerned, it presumably arose from an ancestral cortex- or lichen-eating habit of the type ascribed above to the predecessors of *Aslauga.*

But unlike *Aslauga,* the larvae of *Gerydus* and their attendant *Dolichoderus* ants maintain a mutually friendly relation based on a supposed hypodermal secretion which ants eagerly lick from the surface of the caterpillar's body in general. This ant constructs its nest at the foot of the tree, and consequently can not build the caterpillar into its nest as is done quite incidentally by the arboreal ant associated in a hostile way with *Aslauga.* However, the *Dolichoderus* does persuade the *Gerydus* caterpillar to crawl down the tree trunk into its nest, where it pupates, but this is not accomplished until the larva is full grown. Several arguments can be suggested that may explain why this intranidal phase of life is not commenced while the caterpillar is still immature, as is done in the instance of the phyto-predacious Lycaenas. First, it is possible that the younger larvae yield a small amount or a relatively unpalatable quality of secretion. As a result, the ant would make no effort to remove them to its nest that is situated several yards from their feeding place in the tree top. Second, the larvae may be obligate predators with little or no flexibility in the matter of choosing food. In that case, the larvae would resist any effort the ant might make to remove them from the locality of their prey. Third, in order to enable the larvae to survive and grow up in the nest, the ant would need to provide the customary prey species, and this could not be accomplished unless the plant food of these species could be made available in the

nest. If this were possible, it is probable that the ant would now transport aphids and coccids to its abode for its own use as "cows." But if once brought into the nest, the immature larvae might be capable of utilizing the ant brood as food, as is done by the phyto-predaceous Lycaenas, providing they possess sufficient adaptability in taste sense.

Stated positively, the removal of the larvae is successful when they are mature: first, because the question of food is then no longer involved; second, their secretory glands are probably developed then to their most functional state, as a consequence of which they are more magnetic or desirable as a source of ant confection; and third, the normal restlessness that characterizes mature caterpillars and prompts them to wander about in search of a suitable situation for pupation is a condition of which ants may take advantage in order to facilitate the introduction of the *Gerydus* caterpillar into their nests.

Several higher evolutionary grades of entomophagy may now be described briefly. The step next higher than the *Gerydus* and *Aslauga* predatism is exemplified by the glandless lycaenine *Megalopalpus zymna* D. and H., which shares the nest of a *Pheidole* species and preys upon the ant's homopterous guests. As in the instance of *Aslauga,* caterpillar and ant have a common but conflicting gastronomic interest in the inquilinous Homoptera. However, *Megalopalpus* is one step farther removed from the cortex- or lichen-eating level than *Aslauga* in that it preys on saltatorial Homoptera of the families Cicadellidae and Membracidae instead of sessile Coccidae. What would seem to be an insurmountable difficulty in capturing their agile prey is overcome by the trick of simulating with their forelegs the stroking activities employed by ants when they induce an aphid to emit honeydew.

In its evolutionary standing, *Lachnocnema bibulus* Fabr., another lycaenine species, exceeds *Megalopalpus* in the fact that it not only preys upon the nymphs of cicadellid and membracid guests of the *Pheidole* host but also

drinks the fluid excretions directly as they are yielded from the anus of these nymphs. In imbibing the anal fluids, the *Lachnocnema* caterpillar approximates the habit of the host ant which makes use of the same honey-dew in feeding its larvae and itself. As in the case of *Megalopalpus,* the *bibulus* larva employs the ant's stroking tactics in solving the presumed difficulty inherent in the task of securing the saltatorial nymphs or their excretions as food. Assuming that the present excretophagy is a higher development than the predatism displayed here, how may the derivation of the former from the latter be explained? The answer seems to lie in the fact that the caterpillar is in reality a dualistic feeder, which signifies that no broad gap or basic difference actually exists between the two kinds of food matter taken by the *bibulus* larva. The bodily tissues and the anal excretions of the growing suctorial nymphs of these homopterous families are presumably quite similar in their physical and chemical nature and therefore of equal food value to the larva.

One of the peaks in this developmental series seems to be represented by the liptenine species, *Euliphyra mirifica* Holl. Like *Aslauga, Megalopalpus* and *Lachnocnema, Euliphyra* is associated with ants and lacks the ant gland and eversible tubes. The host is the tree ant, *Oecophylla smaragdina,* which was observed to attend aphids and coccids living outside of its nest. But the *Euliphyra* larvae are intranidal, and, strange to relate, were fed orally on material regurgitated by the ant. How may this friendly treatment of the glandless and protected carapace-bearing *Euliphyra* larva have originated from the earlier homopterophagous habit? Consistent with the theory of evolution advanced here, it must be assumed that the caterpillar of *Euliphyra* or its immediate ancestor once fed upon some kind of homopterous inquilines of the ant. The fact that the Homoptera in this instance lived extranidally is probably to be traced to the failure of the ant to incorporate them when it constructed its nest. Whether this neglect was accidental or habitual, it may

perhaps be said that the ant was less interested in them than is usual in such triangular interrelations involving Lycaenidae. It is possible that this type of attitude of ant toward honeydew-yielding Homoptera is traceable to the aggressive intervention of the *Euliphyra* larva. By virtue of such aggressiveness and its rather extremely developed proboscis-like mouthparts, which certainly encouraged the interoral mode of feeding observed here, the larva has displaced the usual homopterous guests and injected itself into the affection of the host ant. As a consequence, the caterpillar has now become the preferred object of the ant's maternal devotion, while the Homoptera serve a more exclusively utilitarian purpose without receiving in return the protection and care usually accorded the homopterous member of these bionomic triangles.

Finally, mention should be given *Liphyra brassolis* Westw., a member of the subfamily Liphyrinae. Its distinction lies in its use of ant larvae as food. Dodd states it preyed on the grubs of the tree ant, *Oecophylla smaragdina,* in Australia in a nest that contained no homopterous inquilines. However, these ants are otherwise reported to incorporate Coccidae in their nests. The myrmecophagy in the instance noted may have been only a temporary expedient compelled by the absence of the usual homopterous prey species. Nevertheless, the capacity of the larva to adopt more than one type of insect prey indicates that the *Liphyra* larvae are characterized by a considerable flexibility in taste, what may here, as elsewhere among homopterophagous Lepidoptera, be designated opportunism in their food choices. New food habits may therefore be initiated and established by irregularity in the availability of the accustomed food materials which compels the larva to make use of second choice substances then at hand. Accordingly, the instance of myrmecophagy reported for *Liphyra* by Dodd may probably be explained as a direct derivation from the homopterophagy common to this entire series of Lycaenidae.

In concluding this analysis of a few species of homopterophagous Lycaenidae, it should be noted that the examples chosen come from a number of diverging subfamilies and may therefore not be regarded as forming a linear evolutionary series of directly related forms. The bionomic features which the several species have in common rather constitute parallel developments, each of the more complex instances cited constituting the final or subfinal result of an independent line of evolution.

The Phyto-predacious Group

This comparatively small bionomic group consists of a few species of the genus *Lycaena, sensu latu.* It is set off from the above homopterophagous group because it is believed to have an entirely different and independent origin. The known examples are the European *Lycaena alcon* Schiff., *L. euphemus* Hbn. and *L. arion* L. Their phyto-predatism probably represents an outgrowth of the wholly phytophagous habit that still predominates in the family. With few exceptions, the nearest relatives of the phyto-predators resemble the latter in having the ant gland and eversible tubes well developed in most of the larval instars. The larvae of *alcon, euphemus* and *arion* are distinct in that they eat plant tissue only during their earlier instars and turn predatory in the later stadia. While they resemble most of the homopterophagous group in being intranidal they differ from them in utilizing the larvae of their host ants, species of *Myrmica* and others, as prey.

What explanation may be offered for the remarkable transition from phytophagy to myrmecophagy within the larval life of these species? The problem resolves itself into three phases. First, the friendly relation known to exist between ant and caterpillar is obviously to be traced to the attractive secretion which the larva is fitted to produce. Second, the shift from aerial parts of plants to the subterranean nests of ants is readily accounted for by the same fact—the ant's strong appetite for the honey yielded

by the caterpillar. However, while ants attend the larvae of many glanduliferous Lycaenidae quite insanely, they are known to induce but few to leave their food plant in favor of the nests of associated ants in the midst of their developmental stage. The special treatment accorded the phyto-predators could be the result of a more than ordinarily potent acquisitive instinct in the attendant ants, but it is more likely that these particular larvae yield a larger amount of a more palatable quality of honey than their wholly phytophagous relatives. The fact that the phytophagous phase of the larval life is terminated in that instar in which their gland is largest and most functional and not in the earlier instars when the larvae would doubtlessly be more easily managed by the ants, affords factual support for the latter theory. Further confirmation is found in the observations that the ant plays an aggressive rôle in effecting the transition from plant to nest. This act is quite obviously a consequence of the ant's normal instinct to bring into convenient proximity any organism from which it can obtain food substances that gratify its predilection for sweet fluids.

However, it is not denied that the reactions of the caterpillar itself may contribute toward its abduction by the ant. The "hunching up" action of the *arion* larva is interpreted by Frohawk as an invitation to be carried away by the *Myrmica* ant. Moreover, some species of glanduliferous phytophagous Lycaenidae exhibit a negative phototropism, expressed by their nocturnal feeding on plants and their diurnal periods of rest in the nests of ants. Such daily cyclic activity meshes with the diurnal proclivities of ants. While a negative phototropism has not been reported for the contemporary phyto-predators it is possible that such was exhibited in their ancestors and that ants then took advantage of this response which facilitated the transfer of the honey-yielding larvae to their nests.

Third, how may the conversion of phytophagy into myrmecophagy be accounted for? Fundamental to the

answer is the fact that the *Lycaena* larva is still immature when it is kidnapped by the ant. Whether the removal is voluntary, invited or compelled, the larva not only finds itself in a strange habitat but faces the truly grave necessity of securing a substitute for the plant food which it utilized up to that hour. But the usual plant foods are neither available in the new situation nor is the ant capable of supplying them. Rather than starve, the larva makes use of the most available and abundant organic substance—the brood of the host ant.

It is improbable that the transition from phytophagy to myrmecophagy was abrupt or initiated *de novo*. It may be suggested that cannibalism, which occurs widely in this family, constituted the starting point of the predatism. Frohawk states the significant fact that the larvae of *arion* readily devour others of their kind during their phytophagous instars and cease this practice entirely when they later prey on the brood of their host ant. That is, the larvae exhibit from the beginning an inclination or capacity to ingest animal tissue. In a sense, the full-fledged predatism observed in the later instars may therefore have arisen as an expansion of the antecedent cannibalism.

Parasitism and its Rise

Excepting two doubtfully entomophagous species known to the writer, the parasitic Lepidoptera fall into the families Blastobasidae, Heliodinidae and Epipyropidae. These are consistently small to minute in size and restrict their attack to members of the order Homoptera as do almost all the most authentic cases of predacious Lepidoptera.

Zenodochium coccivorella Ch., a blastobasid, and *Euclemensia bassettella* Cl., a heliodinid, parasitized Coccidae of the genus *Kermes*. The entire larval life of an individual is passed within a single *Kermes*, and the host's substance seems to be barely adequate in amount to sustain the parasite until it is full grown. In other words,

the parasitism of these micromoths represents a very low type that has proceeded but slightly beyond the level of predatism. Were the hosts somewhat smaller, the caterpillars would be compelled to move from the first to one or more other *Kermes* scales to secure enough food to complete their growth. In that case, these species would have been rated as predators. This parasitism is therefore but a slightly elevated form of predatism and doubtlessly evolved directly, by a short upward step, from the grade of coccidivory described above as predominating among entomophagous members of this order. The basic distinction between entomophagous predatism and parasitism lies then in the relative size of the offending and offended insect, or entomophag and its prey or host. Secondarily the parasite lives a sessile life as a consequence of its more or less apodous form, whereas the predator must necessarily possess locomotor organs to secure its scattered or elusive prey.

But the parasitism exhibited by the Epipyropidae had a history wholly apart from that of *Zenodochium* and *Euclemensia.* This conclusion is suggested by two bionomic features of the family. First, the hosts of the Epipyropidae, while always Homoptera, are almost invariably members of the saltatorial families Fulgoridae, Delphacidae and Cicadellidae. The exception is *Epipomponia nawai* Dyar, which lives in part on Cicadidae. Second, the epipyropid larvae feed on the fluid anal excretions of the host and not its living body. In doing so, they lie on the dorsum of the host's body and beneath its wings. These larvae are therefore not truly parasitic if judged by the primary criterion that parasites feed upon the vital substances of their hosts. Since they ingest lifeless discarded waste matter, the larvae should rather be classed as high-grade scavengers. However, they are parasitic secondarily in that they derive shelter and transportation from their hosts.

What were the probable antecedents of this parasitoscavengerism, and how may the latter have evolved from

them? The zygaenoid relatives of Epipyropidae are phytophagous and also possess secondary sucker feet that are perhaps homologous with similar structures known on some epipyropid larvae. These facts suggest that the ancestors of modern Epipyropidae were leaf-eaters. It remains then to explain how this semi-parasitism developed from the phytophagy of earlier Epipyropidae. The best clue to the answer seems to exist in the fact that the hosts are exclusively Homoptera and that Homoptera are, themselves, like the ancestral Epipyropidae, phytophagous. This mutual food habit may have been the lodestone that drew the two groups into the same microcosm. Obviously, proximity is one of the principal factors that induce one group of organism to adopt another as food. Why Homoptera and not some other complex of insects was chosen by the micromoths seems to be explained by the simple truth that Homoptera are, on the whole, the most abundant, most omnipresent, and, by virtue of their small size and soft bodies, the most available plant-eating forms. This means essentially that the Epipyropidae took advantage of that edible matter which chanced to occur at hand. However, chance or opportunism was limited or supplemented by certain structural modifications which appeared in the larval form. The transition from phytophagy to parasitism was probably favored by the subcampodeiform body, which is exemplified by *Agamopsyche threnodes* Perk., and the clasping organ known on the anal prolegs of *Epipyrops eurybrachidis* Fletch. The latter enables the larva to stand up on its caudal end and explore for passing hosts, while the campodeiform type of larva is naturally more fleet-footed and aggressive than the eruciform type. These structural advantages probably encouraged their possessors to employ them in the pursuit of their livelihood. By such means, the slow-moving, leaf-eating ancestral epipyropid caterpillars could have become capable of overtaking the active hopping Homoptera that prevailed in their midst.

It is perhaps also very significant in explaining the origin of this parasitism that the food derived from the host is plant sap, which has probably undergone but little physical or chemical change in its passage through the alimentary tract of the Homoptera. This is equivalent to saying that the epipyropid parasites still ingest food of a type that differs at most in only secondary respects from the plant tissues eaten by their phytophagous ancestors. Whether derived directly from plants or indirectly as anal excretions, these plant materials are largely fluid in character, hence no notable change in the structure of the mouthparts has been necessary to adapt the larva to adopt its present food practice.

This transition in food habit was doubtlessly accomplished gradually over a long time. Accordingly, and judging by structural modifications, it is probable the first epipyropid larva to forsake the original plant tissue-eating habit secured the homopterous excretion after it had been dropped upon the leaves of the food plant. From this step in the evolution of the parasitism, the larvae next became better fitted by the acquisition of a cursorial form to pursue the hoppers and thus secure the fluids directly as they were eliminated from the anus. Such a practice has actually been observed in the case of the lycaenid, *Lachnocnema bibulus* (p. 17). The appearance of the caudal clasping organ could easily have enabled the larva to take the final step toward complete parasitism, wherein it took hold of the resting or passing Homoptera and secluded itself beneath their wings to live as an external parasite. Here the caterpillar is not only in position to imbibe the fluids directly from the host as they are excreted but secures in addition the advantages of shelter and transportation.

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SHORTER ARTICLES AND DISCUSSION

FURTHER STUDIES ON WATER ABSORPTION BY REPTILE EGGS[1]

It has already been shown (Cunningham and Hurwitz, 1936) that certain of the turtle eggs as well as those of the pine lizard absorb water during embryonic development. Rather unexpectedly, the lizard eggs absorbed more water, in proportion to their weight, than did those of the turtle. It seems desirable, therefore, to extend the study of other species of turtles. We were fortunate, through the kindness of the Wyandanch Country Club near Smithtown, Long Island, in securing a rather large number of snapping turtles (*Chelydra serpentina*) and a still larger number of the painted turtles, *Chrysemys picta*. The collecting grounds in the immediate vicinity of the Biological Laboratory furnished an ample supply of the box turtle (*Terrapene carolina*).

A newly made nest of the snapping turtle provided the twenty eggs used in the following experiment. The newly laid eggs were carried to the laboratory, numbered and weighed individually. They were then buried in sand and allowed to incubate at room temperature. From time to time they were removed from the incubation boxes, the sand carefully brushed off, and the eggs weighed.

On June 4, when the eggs were taken from the nest the average weight was 9.055 gr. On June 18 the average weight had risen to 10.707 gr.; on July 20, to 11.549 gr.; and on August 14, to 13.171 gr. At the time of this last weighing two embryos were found to be dead and were not included in the average.

The development of the embryo is not so rapid in the laboratory as it is out of doors, and it is difficult to predict the hatching time. It is unfortunate, therefore, that we guessed the turtles would begin hatching about the 6th of September, and planned our last weighing for September 4. When we examined the eggs on the latter date we found that all the eggs except five had either hatched or the shells had been pipped. Since these five eggs showed a considerable gain in weight as compared to the last weighing we are giving here their complete data (Table 1).

[1] The authors wish to express appreciation to the Conservation Department of New York State for the license to collect the turtles used in these experiments.

TABLE 1

Egg no.	Orig. wt.	6/18	7/20	8/14	9/4
1	9.870	11.415	12.147	14.180	18.420
3	9.490	11.280	11.900	13.460	15.855
6	10.965	11.243	12.070	13.625	17.130
10	9.950	10.540	11.302	11.805	13.835
13	10.373	10.420	11.430	13.000	15.410
Average	10.129	10.980	11.769	13.214	16.125

Average increase in weight, 59 per cent.

From these data it is evident that the water absorption is much more rapid in the later stages of development, and in snapper eggs one may expect a maximum increase in weight of approximately 60 per cent. during incubation. That but little of the water absorbed is incorporated into the embryos is evidenced by the fact that the average weight of the newly hatched snapper is 10.1 gr., while the average weight of the eggs is 9.055 gr., in other words not more than 12 per cent. of the weight of the embryo is due to the water absorbed. What use is made of the additional water is to be discussed later.

The study of the box turtle eggs (in which we were assisted by Miss Faith Conklin) was not as satisfactory, for they developed far more irregularly. The death rate was also much higher for some unknown reason. The average weight of 24 of these eggs taken from the oviducts was 9.24 gr. The average of the maximum weights attained was 11.60 gr. The data do not lend themselves to tabulation, since the maximum for some of the eggs was reached before the 60th day of incubation, while one egg reached its maximum on the 109th day. The others were scattered between these two extremes.

The average maximum gain in weight, 28 per cent., is considerably less than that found in the other species reported here, as well as in those reptile eggs previously studied. Contrary to the findings on the snapper and painted turtle eggs, which gained considerable weight during the latter part of the incubation period, the box turtle eggs lost weight rapidly just before hatching, as did the lizard eggs previously studied.

Measurements were also made of these eggs, but since space does not permit their tabulation we may say that the increase in size was comparable to the increase in weight.

The painted turtle gave more satisfactory results than the box turtle. More eggs (121) were available, and although the death rate was rather high in the early development, due possibly to the

fact that uterine eggs were taken and the shell may not have been completely formed, we were able to carry 70 of them to a weighing after 40 days of incubation at room temperature. Between this and the next weighing, 25 days later, 13 more had died. We made a poor guess as to the time hatching would occur and when we began our final weighing we found that all but 40 had either pipped the shell or were hatching.

The eggs were set in two groups, one on June 7, the other on June 27. The data are tabulated in Table 2.

Without some explanation the table is difficult to understand. Thirty-four of the eggs set on June 7 appeared to contain live embryos on July 20. Between this date and August 14 seven of these died, leaving us 27 eggs which appeared normal. To compare the average weight of these eggs with the average for all the eggs originally set did not appear to us as accurate. In the second transverse column under June 7, we have set down the calculations for these 27 eggs for each weighing. When the last weighing was made on September 4, the eggs had already begun to hatch and only 14 were unhatched or unpipped. The data for these we have placed in the third transverse column under June 7. We have also set down the percentage gain over the original weight for these 14 eggs. A similar plan was followed with the eggs set on June 27.

The data indicate that the average gain in weight during incubation is in the neighborhood of 70 to 75 per cent. It is to be noted, as in the snapper eggs, a great portion of the gain in weight is made in the latter part of the incubation period. As in the snapper only a small amount of the absorbed water is used in the body tissue.

The function of the absorbed water seems to be manifold. In the first place a part of it is actually used by the embryo for body fluids as is evidenced by the fact that the newly hatched embryo weighs somewhat more than the original egg. In the second place it keeps the flexible shell fully distended, thus avoiding any localized pressure upon the embryo. In the third place it appears as if the rapid increase of water absorption near the close of incubation is a device for rupturing the eggs. This method of hatching among reptiles has already been mentioned by others, but we have additional evidence in both the snapping turtle and painted turtle eggs which we have observed hatching. The split of the egg shell in these eggs occurs as often in the region of the poste-

TABLE 2

INCREASE IN WEIGHT OF TURTLE EGGS DURING INCUBATION
Painted Turtle—*Chrysemys picta*

	Average Weights								
No. Set	Orig. Weight	July 7 Weight	Increase	July 20 Weight	Increase	Aug. 14 Weight	Increase	Sept. 4 Weight	Total Increase
Date Set: June 7			Per cent.		Per cent.		Per cent.		Per cent.
34	5.706	6.045		6.400	12				
27	5.754	6.110	6	6.444	12	7.514	30		
14*	5.783	6.176	7	6.501	12	7.852	36	9.996	73
Date Set: June 27									
36	5.514	none taken		6.473	17				
30	5.734	none taken		6.458	12	7.196	25		
26**	5.780	none taken		6.435	11	7.140	24	8.784	51

See text for an explanation of this table.
* This small number is due to the fact that the turtles had already begun to hatch when the last weighing was made.
** Most of these eggs had hatched or were hatching when a weighing was attempted on Sept. 9th. Three unhatched eggs on this date had gained an average of .400 g in the 5 days, a total gain of 73 per cent. over their original weight.

rior end of the enclosed animal as of the anterior. Before hatching the calcareous deposit has almost completely disappeared and the remaining envelop has lost its toughness. In these late stages handling often breaks the egg.

Perhaps a word should be said about the importance of the mucus covering the shell in relation to water absorption. Just how it functions we do not know, but we have observed that if the mucus is washed off, the eggs fail to absorb water. While this has not been verified for all species studied, it has been for several of them.

That the absorption of water has little to do with the liquefaction of the albumen is evidenced by the fact previously reported (Cunningham, 1923) that the water absorption, in *Chrysemys cinera,* is minimal during the first few days when liquefaction is occurring. Weights taken of *C. picta,* box turtle and snapping turtle eggs yield the same kind of evidence. This leaves the causal factor of liquefaction undetermined; but that it is an essential feature for development is evidenced by the fact that eggs in which it does not occur fail to develop. Whether or not the live embryo is responsible for the liquefaction is unknown.

These studies, along with the earlier work of the senior author (Cunningham, 1923) and that of Cunningham and Hurwitz (1936), cast considerable doubt upon Needham's (1931) interpretation of the function of the water used by certain turtles in digging their nests. Beyond doubt such water would disappear before the increase in weight of the eggs begins. Furthermore, in the animals studied, evolutionary position and water absorption rates can not be correlated as shown in Table 3.

TABLE 3

Animal	Location of nests*	Av. Maximum Gain in Wt.
Sceloporus undulatus	Open fields	104 per cent.
Terrapene carolina	High grassy fields near woods.	28 per cent.
Chrysemys picta	Wooded hillsides near water, but considerably above water level of lake	70–75 per cent.
Chelydra serpentina	Sand banks, usually well above water level of nearby lakes	60 per cent.
Malaclemys centrata	In sand, a little above high tide levels	47 per cent.
Caretta caretta	Sand dunes	50 per cent.

* While these do not necessarily include all locations where the various kinds of eggs may be found they represent those in which we collected most of the eggs taken from nests.

While we do not doubt that some mineral salts are absorbed,

as suggested by Karashima (1929), we believe that by far the greater part of the increase in weight is due to the water absorbed.

BERT CUNNINGHAM
ELIZABETH HUENE

COLD SPRING HARBOR BIOLOGICAL LABORATORY
AND DUKE UNIVERSITY

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A NOTE CONCERNING THE ADAPTATION OF GEOGRAPHIC RACES OF LYMANTRIA DISPAR L. TO THE SEASONAL CYCLE IN JAPAN

MY work on the geographic variation of *Lymantria dispar* L. led, among other results, to the conclusion that some of the characteristic hereditary differences between geographic races are of an adaptational nature. They adapt the race to the special climatic conditions of the habitat. To be more exact, they harmonize the life cycle of the animal, especially the feeding season and the diapause, with the seasonal cycle of the inhabited region. The characters for which this racial adaptation was analyzed in detail are: (1) The peculiarities of the so-called sex races (see discussion Gen. d. Geogr. Var. III. Roux Arch. *126,* p. 304 ff.). (2) The length of the diapause (see Idem V. l.c. p. 748 ff.). (3) Length of larval stage (see Idem VI. Roux Arch. *130,* p. 292). The major regions in Japan which contained groups of similar races were the island of Hokkaido, northernmost Japan, northeast Japan down to the Gifu-Nagoya region, southwestern Japan. Within these larger groups some regions appeared which showed special characters. In addition definite borderlines were found which separated major groups of races. Some of these lines were rather strange. Thus the northwest corner of Lake Biwa was the seat of races different from the southwestern shore. The Gifu-region belonged to the northeastern part of the country, but the adjacent Nagoya region seemed to belong to the southwestern Japanese group. The region near the Japan Sea was different again.

When I tried to relate the specific features of the races to specific climatic conditions it turned out that for some important points, especially the position of sharp lines of demarcation, the meteorological tables did not furnish any clue. It could be shown, however, that the postulated climatic regions actually existed and were known generally and were also observed by myself, though the tables showed a continuous change from northeast to southwest for the individual climatic features. It would of course be more satisfactory not to rely upon general, not quantitatively measurable features, in checking racial distribution against climatic conditions. This is now possible for just those borderlines which were revealed by the racial distribution but not by the data of the meteorological tables. The intention of this note is to mention the new climatological evidence which puts my earlier conclusions regarding the adaptational basis of the aforementioned characters on the safer basis of data which are recorded quantitatively.

The new material is furnished by T. Seki and has been published within a paper by L. G. Scheidl (Mitt. Deutsch. Ges. Natur-Voelkerk. Ostasiens v. 30, 1937). Seki studied the types of soil in Japan. These again are dependent upon definite climatic conditions (moisture, temperature, etc.), conditions which are actually best expressed in terms of the seasonal cycle. He distinguished three main groups of soils, red, brown and gray ones and Scheidl's paper contains Seki's map. These three soil (and climatic) regions actually coincide with the three major regions found in regard to the adaptational traits of the races of the gypsy-moth: The southwestern group, with a borderline to the east running right across Lake Biwa and through the Gifu-Nagoya plain. The northeastern group up to Sendai on the Pacific side; and the northwestern group, containing mostly the part of the main island adjacent to the Japan Sea. It is especially the direction of the borderline running through Lake Biwa and the Nagoya plain which coincides so beautifully with the dividing line of major races, though nothing of this line is indicated in the meteorological tables. These facts may also serve to caution against statements concerning lack of climatic differences between adjacent regions containing different races, with consequent negative conclusions regarding the adaptational character of traits of geographic races. A definite climatic borderline may exist which is not discernible in the ordinary type of data and which turns out only when the climate as a whole is studied.

RICHARD GOLDSCHMIDT

UNIVERSITY OF CALIFORNIA

THE SILICON CONTENT OF GRASSES[1]

SINCE silicon is the second most abundant element on earth, it is not surprising to find it in nearly all plant and animal tissues. Whether the silicon merely accumulates in the tissues or has a useful function would be very difficult to prove.

It is probable that, during primitive stages of development, organisms have made use of various elements merely because they were present in the environmental medium. Later these elements became part of the characteristic composition of resulting species. An example is the well-known relation of the concentration of inorganic elements in the sera of animals to their concentration in sea water.

The list given in Table 1 may possibly furnish some evidence

TABLE 1

SILICA CONTENT OF GRASSES

Scientific name	Common name	Silica
		per cent.
Agropyron Smithii Rydb.	western wheatgrass	2.1
Agropyron Griffithsii Scribn. and Smith	Griffith's wheatgrass	4.4
Agropyron cristatum (L.) Gaertn.	crested wheatgrass	1.7
Agrostis perennans (Walp.) Tuckerm.	autumn bent	3.3
Agrostis exarata Trin.	spike redtop	2.0
Alopecurus pratensis L.	meadow foxtail	1.8
Andropogon scoparius Michx.	little bluestem	1.3
Axonopus furcatus (Flugge) Hitchc.	carpetgrass	2.4
Beckmannia syzigachne (Steud.) Fernald	American sloughgrass	2.3
Bouteloua gracilis (H. B. K.) Lag.	blue grama	3.5
Bromus anomalus rupr. (*Bromus porteri* Nash)	nodding brome	1.1
Bromus inermis Leyss.	smooth brome	4.9
Buchloe dactyloides (Nutt.) Engelm.	buffalo grass	3.8
Calamagrostis inexpansa A. Gray	northern reedgrass	3.3
Cynodon dactylon (L.) Pers.	Bermuda grass	1.1
Dactylis glomerata L.	orchard grass	1.8
Elymus canadensis L.	Canada wild rye	3.5
Eragrostis curvula (Schrad.) Nees	"Blousaad gras"	0.8
Festuca elatior L.	meadow fescue	2.9
Festuca rubra L.	red fescue	1.8
Festuca obtusa Spreng.	nodding fescue	3.8
Hordeum nodosum L.	meadow barley	1.4
Lolium perenne L.	perennial ryegrass	3.1

[1] Research paper, No. 490, Journal Series, University of Arkansas.

Lolium multiflorum Lam.	Italian ryegrass	1.3
Manisuris cylindrica (Michx.)	necklace grass	3.5
Melica nitens (Scribn.) Nutt.	three-flower melic	1.4
Panicum texanum Buckl.	Texas millet	2.5
Panicum lindheimerei Nash	Lindheimer's panic	1.5
Paspalum urvillei Steud.	Vaseygrass	1.0
Paspalum floridanum Michx.		2.5
Phalaris arundinacea L.	reed canary	2.7
Phleum pratense L.	timothy	2.5
Poa pratensis L.	Kentucky bluegrass	3.1
Poa ampla Merr.	big bluegrass	1.9
Setaria lutescens (Weigel) F. T. Hubb	yellow foxtail	0.6
Sorghastrum nutans (L.) Nash	indiangrass	4.9
Spartina pectinata Link.	prairie cordgrass	1.6
Sporobolus flexuosus (Thurb.) Rydb.	mesa dropseed	1.1
Sporobolus giganteus Nash	giant dropseed	1.0
Sporobolus wrightii Munro	sacaton	0.5
Triodia stricta (Nutt.) Benth.	strict triodia	2.7
Uniola latifolia Michx.	broadleaf uniola	1.4

that silicon in grasses is not merely a fortuitous accumulation. The silicon content of grasses was found to vary widely in the different species, even though these grasses were not grown in their natural habitats, but were all grown from seeds in pots of identical soil under controlled conditions in the greenhouse.[2]

All grass samples were carefully washed, dried to constant weight at 110 degrees centigrade, and silicon determined. The mean values of duplicate analyses are expressed as per cent. of SiO_2 in the dried grass. Perhaps not much can be said concerning the significance of these results, but it is hoped that they may stimulate some interest in the possible rôle in biology of an element which has been neglected by investigators.

A. R. PATTON

UNIVERSITY OF ARKANSAS

[2] Grasses were grown and identified by E. L. Nielsen Department of Agronomy, University of Arkansas.